Drivers of Stream Fish Assemblages and Trophic Interactions

A thesis submitted in partial fulfilment of the requirements for the

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By

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For my father, John Fraley

"Swift or smooth, broad as the Hudson or narrow enough to scrape your gunwales, every river is a world of its own, unique in pattern and personality. Each mile on a river will take you further from home than a hundred miles on a road."

-Bob Marshall

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Abstract

Human and environmentally-driven changes in flood disturbance, habitat size, and land cover can affect fish assemblages in streams. However, it is important to understand the mechanisms underlying these so that resource managers can minimize the effects of detrimental perturbations. This is particularly vital for streams that contain endemic, at-risk taxa or species of recreational and economic importance. Therefore, developing functional measures of fish assemblages which summarize energy flow and trophic pathways (e.g., food-chain length) could be useful to quantify the effects of habitat changes on aquatic communities.

To address this, I surveyed thirty headwater Canterbury, New Zealand streams to evaluate fish mass–abundance relationships (size spectra) and stable isotope metrics (food-chain length and carbon range) as functional measures of aquatic ecosystems and their response to the aforementioned habitat factors. I found that these metrics were responsive to increasing habitat size (food chains lengthened), flood disturbance (carbon range and mass–abundance slopes decreased), and riparian land cover types, proving effectual as integrative measures of aquatic ecosystems.

Next, using these newly-vetted metrics, I assessed the effects of small-scale surface water abstractions on fish assemblages and community trophic structure. I found decreased habitat size downstream of water abstractions was associated with lower abundances of large-bodied fishes, shorter food chains, and predatory release for sensitive, small-bodied native taxa.

I then quantified the effects of habitat size and flood disturbance on theorized relationships between fish body mass and trophic position. Here, I found negative influences of these habitat factors on the trophic position of individual fish species, confirming that environmental factors can be as important as fish body size in determining trophic height.

Finally, I identified the specific mechanisms regulating invertebrate and fish trophic height, as well as community biomass through structural equation modelling. I found that flood disturbance negatively affected both the trophic height and biomass of large-bodied non-native salmonids. Additionally, habitat size and land cover types variably influenced the trophic height of small-bodied native fishes and invertebrates, along with algal, allochthonous, invertebrate, and fish biomass.

Overall, my research has advanced understanding of how flood disturbance, habitat size, and riparian land cover affect freshwater fishes and community food webs through modulation of both trophic structure and fish body size. When used in-tandem, fish mass–abundance relationships and stable isotope-derived food-web metrics will be useful measures for monitoring, mitigating, and rehabilitating aquatic communities in the face of pressures caused by land-use change, flow alteration, and non-native species. Thus, these metrics could provide additional tools to inform appropriate management decisions.

Chapter One

Introduction

A beautifully-dappled brown trout caught in a New Zealand backcountry river.

Key Influences on Stream Ecosystems

Understanding how abiotic and biotic factors affect stream ecosystems and fish assemblages is useful for investigating effects of human habitat alteration on aquatic communities. Habitat conditions such as temperature and habitat size affect stream fish feeding behaviour, diet, energy budgets, and trophic structure (Post et al. 2000; Arim et al. 2007). Additionally, factors such as stream size, flood disturbance, riparian land cover, and non-native predator presence influence fish assemblages (McHugh et al. 2010). However, the effects of these habitat components, particularly differing land cover type, are not well-quantified or understood. Therefore, I have reviewed and explored several of the most influential drivers for New Zealand stream fishes in the following sections, and in my doctoral research presented in this thesis.

Stream flow and flood disturbance

In most cases, unmodified flow maximizes connectivity of stream networks for broad-scale energy transfer and subsidies, natural flow variability and flooding, and downstream dispersal of aquatic invertebrates (Bunn & Arthington 2002; Postel & Richter 2012; Datry et al. 2014). In many streams, natural flood disturbance regimes are thought to structure fish assemblages and food webs (Wootton et al. 1996; Davey & Kelly 2007; McHugh et al. 2010). This is because flood-prone streams are harsh environments, typically having lower standing stocks of basal resources due to stream bed shift during floods. This may be beneficial for native taxa however, which are adapted to cope with extremes in flow (Leprieur et al. 2006), which I have investigated further in this thesis. However, natural flow fluctuations are often threatened by human modification and manipulation of watercourses (Poff et al. 1997; Lytle & Poff 2004), and because some of the most important influences on streams revolve around flows, flow alteration by humans is a major concern. Therefore, I focused heavily on investigating the effects of flood disturbance on stream fish assemblages in this thesis by

comparing streams across a gradient from flood-prone, braided rivers to relatively stable spring creeks.

Habitat size

Flooding disturbance encapsulates one aspect of stream flow regimes, and is related to fluctuations in discharge, which in turn influences the size of aquatic habitats. Globally, stream food webs are highly dependent on water levels and flow to maximize availability of habitats for biota (Allan & Castillo 2007; Davies et al. 2014), with dewatered streams typically displaying shrunken aquatic spaces. The size of habitats available for freshwater fishes can be important in determining abundance, biomass, and possibly trophic structure within assemblages (McHugh et al. 2010; Sabo et al. 2010). Although it has been found that increased habitat size does not increase per unit area productivity in New Zealand streams (McIntosh et al. 2018), larger habitats should have increased total biomass of fish per unit stream length because there is more productive space in a larger habitat that should lead to a greater abundance of prey (Vander Zanden et al. 1999). However, there is some debate about whether habitat size influences trophic structure of stream communities (Post et al. 2000; Sabo et al. 2010). If habitat size is an important influence on food-web structure, human-caused habitat size reduction from damming, water abstraction, and diversion in streams may be problematic (Falke et al. 2011), likely affecting fish assemblages (McHugh et al. 2015). In New Zealand, the most common type of flow modification that results in habitat size reduction is water abstraction for agricultural purposes. Therefore, I examined both the effects of natural habitat size gradients (ranging from streams that were mere trickles to large, waist-deep rivers) and the effects of dewatering due to anthropogenic water abstraction in my research.

Land cover and land-use change

In addition to the effects of flooding and habitat size, riparian and catchment land cover can affect stream ecosystems. Intact riparian cover is beneficial for streams through buffering of water evaporation and stream temperature, contributing detritus, and affording cover for aquatic biota (Baxter et al. 2005). Additionally, unaltered vegetative cover throughout a catchment allows for buffering of erosion, precipitation events, and sediment input into streams (Sutherland et al. 2002). However, as human populations expand, freshwaters come under increasing threat from the negative influences of human development near riparian zones and within catchments. This typically manifests as land-cover change and removal of riparian vegetation, which causes increased solar radiation and evaporation to occur (Moore et al. 2005; Richardson et al. 2007). This can lead to decreased habitat size, less allochthonous input, and increased water temperatures (Li et al. 1994; Naiman and Decamps 1997), detrimentally affecting fishes and often opening the door for exotic species to invade (Dudgeon et al. 2006). The effects of different land cover types on aquatic communities in New Zealand have not been well-explored in the context of fishes, especially at the catchment scale (Hanchet 1990; Jowett et al. 1996). Therefore, in complement to the aforementioned flow regime factors, I endeavoured to link remotely-sensed land cover to field-measured characteristics of aquatic communities in this research, to better understand these effects.

Non-native predators

Abiotic factors such as land cover and flow are likely influential in structuring stream fish assemblages, but interactions between biota are important as well. For example, predators often structure aquatic food webs in top-down systems (Power 1992; Winkelmann et al. 2011), and the size and abundance of large-bodied predators can give indications of ecosystem health and productivity (Petchey & Belgrano 2010; Hatton et al. 2015; McIntosh

et al. 2018). Large, non-native predators can negatively affect native freshwater fish assemblages and aquatic communities by causing trophic shifts and cascades (Ricciardi et al. 1998; Ellis et al. 2011), often pushing native biota out of habitats and narrowing their feeding niches (Peterson et al. 2004). This is seen in New Zealand where rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) depress native *Galaxias* populations through predation (McIntosh et al. 2010). While trout are well-established in New Zealand waterbodies and managed as sportfish, there is still much latitude for improving management of them for the benefit of native fishes (Jones & Closs 2018). The impact of trout on native fish and invertebrates has been well-documented, but the mechanisms behind this influence, as well as the implications for aquatic ecosystems as a whole, have not been well-explained. Approaches to protecting or rehabilitating indigenous biota could be formulated with this underlying information. To explore this, I assessed the effects of interacting habitat factors on Salmonidae taxa, and subsequently their influence on native fishes within freshwater assemblages. This was facilitated through characterisation and evaluation of fish assemblages and community trophic structure, as discussed in the following sections.

Evaluation of Mass-abundance Relationships and Stable Isotope Analysis as Functional Measures of Aquatic Communities

Ecological networks, including food webs, characterise the interactions of organisms within or even among ecosystems (Ings et al. 2009; Thompson et al. 2012). Because they summarise the transfer of energy, characterisation of food webs can potentially allow researchers and managers to monitor ecosystem health and identify changes that may indicate potential threats (Bunn et al. 1999), such as the ones mentioned in the previous section. In addition, scientists can predict how ecosystems might be affected by various scenarios (climate change, human modifications, etc.) if controls on connections between biota are known (Clements & Rohr 2009). Finally, describing food webs gives resource managers

insight into ecosystem mechanisms and provides a measure of health via identification and monitoring of trophic pathways, giving clues to how existing issues could be corrected (e.g., declining native species abundance or invasion of exotic biota; Lake et al. 2007; Thompson et al. 2012).

Description of food webs, or the detailed resolution of trophic links and interaction strengths, is highly desirable. However, the amount of effort required to catalogue and examine all biota and trophic relationships within even one ecosystem can be prohibitive, or impractical if broad inferences are intended. Thus, recent studies have explored the collection of data that approximates and standardises food webs for simpler comparisons, also known as proxies or functional measures (Hall & Raffaelli 1993; Arim et al. 2010). Predators within an ecosystem are typically large-bodied, drive the interactions and body size structure of subordinate biota, and can be useful proxies to focus data collection on (McCann et al. 2005; Jellyman et al. 2014). In the next section, two possible measures of interest are outlined: mass–abundance relationships (size spectra) that synthesize characteristics of fish assemblages, and trophic structure (via stable isotope analysis) that characterizes aquatic community energy transfer patterns.

Mass–abundance relationships

Mass–abundance relationships (size spectra), or the distribution of abundance of organisms in binned size categories, have been used to characterise and monitor terrestrial, marine, and freshwater food-web structure and health (Cohen et al. 2003; Clauset & Erwin 2008; Gray et al. 2014; Wheeland & Rose 2015). The movement of energy and change in biomass over trophic levels usually results in these predictable size-abundance relationships (White et al. 2007; Petchey & Belgrano 2010; Trebilco et al. 2013). This is because the body size of an organism is related to its metabolic and energetic demands, which in turn affect feeding rates and body scaling (Brown et al. 2004; Woodward et al. 2005).

Measuring body size and abundance of a representative subset of organisms is far less costly and time-consuming than exhaustively quantifying all aspects of a food web (e.g., constructing a metaweb), and can be applied and compared between multiple ecosystems (e.g., river catchments or stream reaches), taxonomic groups (species or other evolutionarily significant units), and functional groups (e.g., herbivores, predators, and omnivores; Petchey & Belgrano 2010; Warburton 2015). Due to factors such as system productivity, metabolic demands of biota, and interspecific interactions, mass–abundance relationships typically follow a right-skewed distribution, with low frequencies of large-bodied organisms and high frequencies of small-bodied taxa (Layman et al. 2005; Warburton 2015). However, this paradigm may be broken in communities with seasonally migratory organisms (e.g., spawning adult Pacific salmon), or those experiencing negative conditions such as habitat size reduction, flow alteration, or invasion of non-native biota, all of which I evaluate in this thesis. Thus, assessing and monitoring mass–abundance relationships within an assemblage can be a useful method for identifying changes to a system that are not clearly evident on the surface (Layman et al. 2005).

Stable isotope metrics

Another common technique used for characterising food webs is stable isotope analysis. Stable isotope (SI) analysis, or the examination of ratios of atoms of one or more elements with different numbers of neutrons, is a useful tool with broad applications for ecology, archeology, geochemistry, and forensics (Richet et al. 1977; Schoeninger & Moore 1992; Fry 2007). In ecology, SI analysis is primarily used as a tracer (e.g., animal origin or migration) or to assess trophic position (TP) and energy transfer in animals and plants (Vander Zanden 1997; Hobson 1999). Trophic position is typically calculated for individual organisms using nitrogen and carbon isotope ratios ($\delta^{13}C$ and $\delta^{15}N$), and organisms with higher TP values are nearer to the apex of an ecosystem's trophic pyramid (Post 2002). The

trophic position of top predators in comparison to values for a standard primary consumer within the same habitat (food-chain length) allows inferences to be made about the structure of an entire food web, and SI-derived TP values are comparable among systems. Trophic metrics have been found to respond to changes in habitat size and flow (Sabo et al. 2010; McHugh et al. 2010), so may be suitable functional measures of ecosystems. Thus, similar to mass–abundance relationships, trophic metrics could be used as an indicator of ecosystem perturbation, and may reveal where mitigation or rehabilitation efforts should be focused. In this research, I evaluate how fish assemblage SI metrics respond to natural and human-induced fluctuations in flow regimes, land cover, and the presence of non-native predator taxa.

Body size and trophic metrics in tandem

Despite the abundance of aquatic food web research using trophic structure and mass–abundance methods individually, there are a limited number of studies linking these two approaches, especially in freshwater ecosystems. A meta-analysis of 8,361 fish confirmed that TP and maximum body size are positively correlated (although SI data were not used; Romanuk et al. 2011). However, a study looking at body size and $\delta^{15}N$ values of northeast Atlantic fishes found that body size predicted trophic level when assessed across multiple species, but was not a reliable proxy of TP within-species (Jennings et al. 2001). Related research examining fishes in a tropical Venezuelan river yielded no relationship between SI-derived TP and body size (Layman et al. 2005), while studies of Uruguayan fishes did find a relationship between non-SI TP and body size of killifishes, and contended that trophic structure was influenced by gape limitation of predators (Arim et al. 2010). If a robust connection between body size and TP of fish could be confirmed, size measurements could be employed broadly as a non-lethal measure of trophic position for ecological investigations, and robust meta-analysis could be undertaken combining results from studies using either

body size or SI methods (Jennings et al. 2001). Because no comparison has been conducted between fish body size and trophic position in temperate freshwater environments, I investigated this link further in this thesis.

Thesis Outline

My overall goal was to investigate the mechanisms behind how flood disturbance, habitat size, and riparian land cover affected the body size, abundance, biomass, and trophic organization of freshwater fish assemblages, to evaluate the usefulness of mass–abundance and stable isotope metrics as functional measures of aquatic communities. If these metrics are reliable integrative measures, they could be utilized by resource managers to influence stream and fishery management regulation and decision-making in the face of threats to freshwater ecosystems. I present my research within four data chapters. Each data chapter has been written as a stand-alone manuscript to facilitate publication in peer-reviewed journals, but are all connected, and are synthesized in the final 'Discussion' chapter. Because of this approach, there is some degree of repetition within the 'Introduction' and 'Methods' sections of several chapters to ensure they are discrete manuscripts. Chapter Two has been published in the journal *Ecology of Freshwater Fish* (Co-authors: Helen Warburton, Phillip Jellyman, Dave Kelly, and Angus McIntosh), and has been re-formatted for presentation in this thesis. I carried out the fieldwork, laboratory work, statistical analyses, and the majority of writing for Chapter Two myself, with study design input and manuscript editing provided by my supervisory committee members/co-authors. In the case of Chapter Three, I equally contributed effort to this investigation in-tandem with fellow PhD student Nixie Boddy, and with input from the members of both of our supervisory teams (Angus McIntosh, Helen Warburton, Phil Jellyman, Dave Kelly, and Doug Booker of NIWA). The remainder of the work in this thesis is my own. Figures and tables are included within each chapter, with one

numbering system running throughout the entire thesis. All references are provided at the end of the thesis to avoid repetition.

To meet my research goal, in Chapter Two I tested the responsiveness of fish mass–abundance relationships and stable isotope metrics (food-chain length and carbon range) to flood disturbance, habitat size, riparian land cover, and predator fish presence in thirty headwater stream reaches within the Waimakariri River of Canterbury, New Zealand. The results of this investigation indicated that the metrics tested were responsive to both abiotic and biotic habitat factors, including habitat size.

Thus, I proceeded to test this further in Chapter Three, where I evaluated the effects of decreases in habitat size downstream of water abstractions on fish assemblages. This investigation was conducted in fifteen stream reaches for each of four different Canterbury, New Zealand streams with surface water abstractions. The study was designed to isolate the artificial effects of abstraction from the natural effects of stream hyporheic exchange on the newly-vetted ecosystem functional measures.

Next, because I had found in Chapter Two that fish trophic metrics (i.e., food-chain length and carbon range) were influenced by habitat size and flood disturbance, I quantified the potential influence of these habitat factors on the theorized relationship between fish body mass and trophic position. This relationship has not been previously examined for temperate freshwater fishes, and identifying the modulators of trophic position would contribute to knowledge of how trophic structure is affected by habitat in ecosystems. Here, I evaluated the mass and trophic position of a subset of fishes, with replication from multiple species, from the datasets collected for Chapters Two, Three, and Five.

Upon confirming that habitat size, flood disturbance, and riparian land cover affected measures of fish trophic structure and abundance, I delved deeper into the mechanisms

behind how these factors affected aquatic community biomass and SI-derived trophic structure in Chapter Five. To do this, I quantified habitat characteristics, fish biomass, aquatic invertebrate biomass, algal biomass, allochthonous biomass, fish trophic height, and invertebrate trophic values for twenty-seven stream reaches from seven river catchments within Canterbury, New Zealand. I then constructed separate piecewise structural equation models for both biomass and trophic height, linking community components together and testing the relationships between them to identify whether the underlying mechanisms were similar for both biomass and SI-derived trophic height of fishes. The goal of contrasting the mechanisms within community biomass and trophic height was to vet measures that managers could employ to set optimal fishery harvest limits and regulations that would conserve fish biomass and aquatic community food-web structure.

Finally, in Chapter Six, I recount the important findings from my investigations. I also describe how what I have found contributes to the fields of freshwater ecology and fisheries science, strategies for using what I have found to inform stream management, and recommendations for related research in the future.

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Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapter Two "Responsiveness of fish mass–abundance relationships and trophic metrics to flood disturbance, stream size, land cover, and predator taxa presence in headwater streams"

Fraley, K. M., Warburton, H. J., Jellyman, P. G., Kelly, D., & McIntosh, A. R. (2018). Responsiveness of fish mass–abundance relationships and trophic metrics to flood disturbance, stream size, land cover and predator taxa presence in headwater streams. Ecology of Freshwater Fish, online-only. https://doi.org/10.1111/eff.12410.

Please detail the nature and extent (%) of contribution by the candidate:

Kevin is the first author on this published scientific article. He developed the study design with input from coauthors, undertook all fieldwork, labwork, and data analysis, and synthesized the findings into a peer-reviewed journal article. He wrote the first draft of the text and likely wrote 90% of the text as a whole. He also handled the entirety of the journal submission process and review, with some input from coauthors on two required revisions. Supervisor Angus McIntosh reviewed and provided suggestions for improvements on several drafts of the article, and other coauthors reviewed at least one draft.

Certification by Co-authors:

The undersigned certifys that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

Name:	Signature:	Date:
Angus McIntosh		23/7/18

Chapter Two

Responsiveness of fish mass–abundance relationships and trophic metrics to flood disturbance, stream size, land cover, and predator taxa presence in headwater streams

The Broken River in the Waimakariri River Catchment, a stream sampled for this Chapter.

Fraley, K. M., Warburton, H. J., Jellyman, P. G., Kelly D., McIntosh A. R. (2018). Responsiveness of fish mass–abundance relationships and trophic metrics to flood disturbance, stream size, land cover and predator taxa presence in headwater streams. *Ecology of Freshwater Fish*, in press. https://doi.org/10.1111/eff.12410

Abstract

Characterisation of food webs, by summarizing energy transfer and trophic relationships, allows more functional measurement of ecosystems and may reveal threats (e.g., land-cover change) in sensitive environments that are not obvious from conventional biomonitoring. However, typical methods used to achieve this are time-consuming and expensive. Therefore, I tested the usefulness of fish-focused food-web proxies as functional measures, specifically mass–abundance relationships of fish assemblages and stable isotope-derived metrics in headwater stream reaches. These metrics have been trialed before for similar use in other settings, but have yielded varying results, and have not been employed in tandem in temperate freshwaters. Sampling reaches (n = 46) were spread across a variety of streams, and the effects of habitat predictors at multiple scales on metrics were assessed using model selection. I found that habitat size positively correlated with food-chain lengths in streams, possibly because of increased abundance of fish at multiple trophic levels in habitats with more space. Additionally, flood disturbance was negatively associated with fish mass–abundance and carbon range, likely due to the harshness of flood-prone streams. Riparian land cover variables were correlated with multiple metrics, indicating the importance of terrestrial-aquatic linkages. Additionally, variations in all metrics were influenced by the presence of native, predatory longfin eels. Overall, I conclude that mass–abundance relationships and stable isotope-derived metrics are sensitive to drivers of trophic organisation and likely reflect processes occurring at multiple spatial scales in freshwaters. Thus, these metrics could be an insightful monitoring tool for managers because they reflect functional measures of aquatic ecosystems.

Introduction

For ecologists, quantifying food webs and trophic interactions is highly desirable because they reflect the flow of energy and biotic relationships (Thompson et al. 2012). Food webs can also respond to a perturbation or a change in the ecosystem (e.g., drought-caused extirpation of sensitive predator species resulting in shortening of food-chain length), which can be quantified by exhaustively cataloguing dietary and productivity measures for each trophic level (Ledger et al. 2013). However, the amount of effort required to catalogue and examine all biota and trophic relationships can be prohibitive, or impractical if broad inferences are required. Thus, methods that approximate and standardise food webs for easier comparison are needed (Arim et al. 2010; Hall & Rafaelli, 1993). Although fishes compose only a subset of the aquatic food web, sampling fishes within freshwater ecosystems could be a useful approach because they are typically large-bodied, occupy higher trophic positions, and often drive the interactions and mass–abundance relationships within communities (Jellyman et al. 2014; McCann et al. 2005). However, it is unclear which fish-related proxies would best-describe patterns and changes in assemblages and food webs, particularly in freshwaters. Several metrics have been considered as suitable candidates for this purpose, including fish mass–abundance relationships and fish-focused stable isotope analysis (Jennings et al. 2002). These metrics have not been utilized in tandem for temperate freshwater food-web investigations previously, but have been shown to respond to gradients in marine and tropical contexts (Layman et al. 2005). Therefore, I investigated the use of stable-isotope analysis and fish mass–abundance relationships to characterise energy transfer patterns and make inferences about freshwater food webs along important environmental gradients.

Mass–abundance relationships (i.e., the frequency of organisms in binned size categories) have been used to characterise terrestrial, marine, and freshwater food-web

structure (Figure 2.1; Clauset & Erwin 2008; Cohen et al. 2003; Gray et al. 2014; Wheeland & Rose 2015). The movement of energy and change in biomass over trophic levels usually results in these predictable size-abundance relationships, which typically follow a right-skewed distribution, with low frequencies of large-bodied organisms and high frequencies of small-bodied taxa (Layman et al. 2005; Petchey & Belgrano 2010; Trebilco et al. 2013). These body size-abundance relationships occur because the body size of an organism is related to its metabolic and energetic demands, which in turn affects feeding rates and growth (Brown et al. 2004).

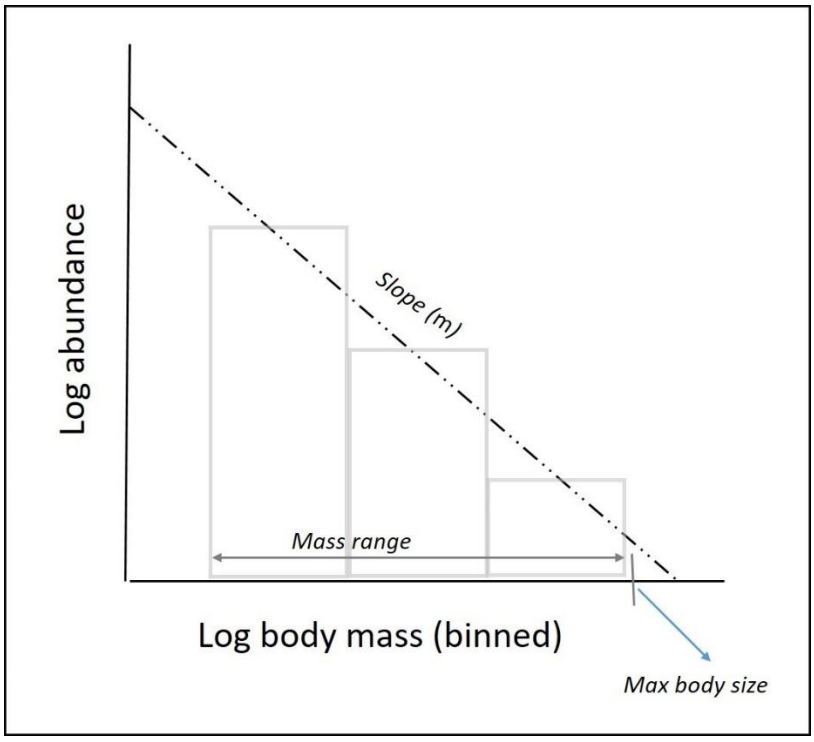

Figure 2.1. Mass–abundance relationship constructed by binning individual fish by body size and creating a frequency histogram. Some metrics used in my investigation are labelled, and include the largest fish by $\log_2$ mass (Maximum body size), the difference in $\log_2$ mass between the largest and smallest fish (Mass range), and the slope of the $\log_2$-transformed mass–abundance relationship (slope) found in each reach.

However, this paradigm may be challenged in communities with seasonally migratory organisms (e.g., spawning adult Pacific salmon), or those experiencing constraints such as habitat destruction, pollution, or invasion of non-native biota. Moreover, measuring body size and abundance of a representative group of organisms like fishes is far less costly and time-

consuming than exhaustively quantifying all food-web interactions (e.g., constructing a metaweb), and can be applied and compared between multiple ecosystems (e.g., river catchments or stream reaches), taxonomic groups (species or other evolutionarily significant units), and functional groups (e.g., herbivores, predators, and omnivores; Petchey & Belgrano 2010). Thus, assessing and monitoring mass–abundance relationships of a fish assemblage could be a useful method for identifying characteristics and functions of a system that are not clearly evident from species abundance patterns (Jennings et al. 2002).

Similarly, stable-isotope (SI) analysis is a useful technique, with broad applications for ecology (Fry 2006; Richet et al. 1977), and is commonly used to assess trophic position (TP; Vander Zanden 1997) and energy transfer through food chains (Post 2002). Trophic position is typically calculated for individual organisms using nitrogen isotope ratios, and organisms with higher TP values are nearer to the apex of an ecosystem's trophic pyramid (Post 2002; McHugh et al. 2012). The trophic position of top predators is determined by comparing the nitrogen isotope ratio of the predator relative to the value for a standard primary consumer within the same habitat (known as food-chain length; FCL). The calculation of TP values for all species allows inferences to be made about the structure of an entire food web and these SI-derived TP values are comparable among similar systems. Along with nitrogen isotopes, isotopes of carbon are also typically measured because the range in carbon isotope ratios (carbon range) among co-ocurring organisms describes the dietary breadth of fishes in an assemblage (McHugh et al. 2012).

Freshwaters are some of the most vulnerable and threatened ecosystems worldwide (Gleick & Ajami 2014; Vörösmarty et al. 2010), and typical methods for providing measures of ecosystem health (e.g., water chemistry or invertebrate indices) reflect only a subset of the aquatic community. Less-common comprehensive measures such as food-web diet studies examining links between all biota are time-consuming and expensive. Therefore, developing

more functional measures of freshwater ecosystem health is necessary (Jennings et al. 2001; Gray et al. 2014). Deforestation and development near watercourses, introduction of non-native species (Boyer et al. 2008), pollution from multiple sources (Chi et al. 2007), a rapidly changing climate (Woodward et al. 2010), and impoundment and stream flow modifications (Malmqvist & Rundle 2002) all contribute to extirpation of native biota and disruption of aquatic communities. Moreover, these factors are often compounding and interacting. Therefore, tools that can assess aspects of freshwater ecosystem function in the face of these threats (e.g., mass–abundance relationships and SI metrics in combination), are badly needed.

I assessed the responsiveness and suitability of fish mass–abundance relationships and SI-derived metrics as integrative measures of freshwater food webs that could be substitutable for more time-consuming and limited comprehensive metrics that are typically used in food web studies. I examined how these measures varied in relation to: 1) river discharge (a proxy for habitat size), 2) flood-proneness (as defined in Methods section), 3) riparian land-cover types, 4) presence of large-bodied predator taxa, and 5) habitat variables of different types and at different spatial scales. Discharge and habitat size affect fish assemblages and aquatic communities by controlling space availability and the rate of prey delivery (McHugh et al. 2015). Similarly, the frequency and magnitude of flood disturbance (flood-proneness) affects aquatic communities by reducing the standing stock of primary producers and aquatic invertebrates, resulting in lower overall productivity and food availability for secondary consumers (Death & Winterbourn 1994; McHugh et al. 2010; Sponseller et al. 2013; Jellyman et al. 2014). Additionally, catchment land cover and riparian vegetation type are important for determining the amount and type of terrestrial food subsidies that may enter aquatic ecosystems, as well as for buffering the connection between land and water (England & Rosemond 2004; Wipfli et al. 2007). Overall, it is likely that abiotic and biotic factors (i.e., predator presence) at multiple spatial scales interact with one-

another to structure fish assemblages and food webs (Fausch et al. 2002; McCann et al. 2005), which should be reflected in mass–abundance relationships and stable-isotope metrics within a diverse catchment.

Given the above relationships, I first hypothesized that greater discharge at the time of sampling (referred to hereafter as 'habitat size') would result in a corresponding increase in fish size range, maximum body size, and food-chain length (*H1*; Table 2.1). Secondly, I expected that increased flood-proneness would result in decreases to fish size range, maximum body size, and food-chain length and a shift towards a shallower slope of the mass–abundance relationship (*H2*). Third, land cover type was expected to affect maximum fish body size, size range, and food-chain length (*H3*). Fourth, body size and SI-derived metrics were hypothesized to increase in response to the presence of large-bodied predators (native eels and non-native trout), with a corresponding decrease in mass–abundance slope (*H4*). Finally, abiotic habitat factors, at local scales (field-measured), would be more important than those at landscape-scales (remotely sensed) in determining fish size and SI-derived metrics (*H5*).

Table 2.1. Hypothesized responses for fish assemblage and aquatic community stable isotope metrics from stream study reaches in the Waimakariri River catchment, New Zealand. Predictions are shown for five response variables in relation to increasing habitat size or flood proneness, variation in riparian land cover, and presence of large predators.

Hypothesis	Response	Prediction
H1: Increased discharge (habitat size)	Mass–abundance slope	No change
	Mass range, maximum	Increase
	Total biomass	No change
	Food-chain length	Increase
	Carbon range	No change
H2: Increased flood-proneness	Mass–abundance slope	Increase (shallower)
	Mass range, maximum	Decrease
	Total biomass	No change
	Food-chain length	Decrease
	Carbon range	No change
H3: Riparian land cover type	Mass–abundance slope	No change
	Mass range, maximum size	Increase with native forest and tussock, decrease with bare ground
	Total biomass	No change
	Food-chain length	Increase with native forest and tussock, decrease with bare ground
	Carbon range	No change
H4: Predator presence	Mass–abundance slope	Decrease (steepen) with presence of both eels and trout
	All other responses	Increase with presence of both eels and trout
H5: Scale and type of variable	All responses	Strongly affected by local-scale biotic and abiotic variables, not affected by broad-scale abiotic

Materials and Methods

Study site and habitat measurements

The Waimakariri River (171°45’29”E, 42°59’39”S) is a braided, glacial-and runoff-fed watercourse in the Canterbury region, South Island, New Zealand (Figure 2A.1; Reinfelds & Nanson 1993). The river has a catchment area of 3,560 km^2, drains the eastern side of the Southern Alps mountain range and discharges into the Pacific Ocean. This river catchment contains a diverse range of surrounding land cover, flood-proneness, and volume. Streams originate in either alpine rock, tussockland, or lower-altitude springs, flow through indigenous forest and scrub, and finally transect pastoral lowlands before entering the ocean (Sohrabinia et al. 2012). My study focused on headwater (within 50 km of the drainage

divide), wadeable, first to sixth-order stream reaches in the catchment spanning as large a range of discharge (0.01 to 4.03 $m^3 \cdot s^{-1}$), flood-proneness, fish species composition, and surrounding land cover as possible.

Fish species present in the Waimakariri River headwaters include a mixture of native and introduced taxa as well as both freshwater resident and diadromous fishes (McIntosh 2000). Notable native taxa include catadromous longfin eels (*Anguilla dieffenbachii*), resident and amphidromous galaxiids (*Galaxias* spp.), and resident bullies (*Gobiomorphus* spp.). Anadromous Chinook salmon (*Oncorhynchus tshawytscha*), brown trout (*Salmo trutta*), and resident rainbow trout (*Oncorhynchus mykiss*) are non-native to New Zealand, and the two trout species are widespread in the catchment (Woodford & McIntosh 2010). There are several avian opportunistic fish predators present, but no piscivorous mammalian taxa, resulting in little top-down control on fishes from the terrestrial environment (Oliver 1955).

Thirty headwater mainstem braid and tributary stream reaches, spread spatially within the upper catchment, were sampled (Table 2A.1). Reaches (50 m in length) were chosen *a priori* by evaluating ease of access whilst maximizing diversity of discharge and flood disturbance, based on previous site views by research group personnel. Fieldwork was undertaken during the 2016 Austral summer (January-February). Supplementary historic data (collected in 1997, 2004, 2005, and 2009) from sixteen additional reaches within the catchment, sampled using similar methods, were included (n = 46 total reaches, Table 2A.1).

Habitat characteristics measured at each 50-m sampling reach (local scale) included the river disturbance index (RDI, a visual measure of flood-proneness; Pfankuch 1975), wetted width (m), average depth (cm), average velocity (m/s), cross-sectional area (m^2), and a one-off estimate of discharge ($m^3 \cdot s^{-1}$; Table 2.2). The RDI is calculated by summing scores from 15 habitat assessment categories, including bed and bank substrate size (capacity for bed disturbance during a flood), periphyton and riparian vegetation cover (time since last

flood), and landform slope and channel capacity (flooding magnitude; Jellyman 2013b; Peckarsky et al. 2014). I have termed RDI as 'flood-proneness' rather than 'flood frequency' or 'flooding potential' because it incorporates multiple elements of flood disturbance (although I recognise that flood proneness does not account for other important hydrological disturbances such as intermittency). Lower RDI scores indicate less flood-prone reaches with more 'stability,' while high scores denote streams with frequent and large floods ('unstable' or 'disturbed'). Discharge was estimated using the velocity-area method with velocity measured using either an electromagnetic (Marsh-McBirney Flo-Mate™ Model 2000) or acoustic doppler velocimeter (SonTek FlowTracker© Handheld ADV), and was measured at the time of sampling only. I was confined to a one-off measurement at each reach because of time and logistical constraints.

Table 2.2. Habitat characteristics measured or calculated for stream study reaches in the Waimakariri River catchment, New Zealand. * denotes variables not included in top models or removed due to collinearity. See Methods for detailed description of datasets and variables. Local-scale variables are denoted by 'S' and large-scale variables are denoted by 'L' in the spatial scale column. Variable type is 'F' for field-measured abiotic, 'B' for field measured biotic, and 'R' for remotely-sensed abiotic (Freshwater Environments of New Zealand).

Spatial Scale	Data Source	Description	Type	Abbreviation	Example or Units
50-m reach (S)	Field-collected	Wetted width*	F	WIDTH	m
		Average depth*	F	DEPTH	cm
		Average velocity*	F	VEL	m/s
		Discharge	F	FLO	$m^3 \cdot s^{-1}$
		River disturbance index	F	RDI	Index
		Eel presence	B	EEL	Y/N
		Trout presence	B	TROUT	Y/N
		Juvenile Chinook salmon presence *	B	CHI	Y/N
740-m reach (average; L)	FWENZ	Sinuosity*	R	segSinu	Index
		Riparian bare ground cover	R	segBare	%
		Riparian tussock cover	R	segTussock	%
		Riparian scrub cover	R	segScrub	%
		Upstream indigenous forest	R	usIndigForest	%
		Upstream pastoral cover*	R	usPastoral	%
		Stream order*	R	ORDER	Integer
		Elevation*	R	ELE	m asl
		Distance from sea*	R	distSea	km

In addition to field-measured (local) variables, I incorporated remotely-sensed and landscape-modelled variables to reflect large-scale influences associated with catchment landcover and landforms, and riparian conditions. The River Environment Classification (REC; Snelder et al. 2004) digital stream layer, and the associated Freshwater Environments of New Zealand (FWENZ), include attributes estimating a suite of landscape-scale (740 m average segment length) habitat characteristics derived from digital elevation models, the New Zealand Land Cover Database, precipitation records, stream flow, and stream network structure (Booker 2010; Leathwick et al. 2008). I extracted variables from REC and FWENZ, chosen *a priori* based on habitat characteristics known to be important to fish populations and aquatic communities at the riverscape scale (Table 2.2; Fausch et al. 2002). These included sinuosity, percentage of riparian bare ground cover, riparian tussock cover, riparian scrub cover, percentage of indigenous forest cover in the catchment upstream of the reach, stream order, elevation (m), and distance from the sea (m).

Fish capture and processing

To measure relative mass–abundance (for 1997, 2004, 2005, 2009, and 2016 samples; McIntosh 2000) and collect a subsample of individuals for stable isotope analysis (2016 sample only), fish were captured at 50-m reaches using single-pass electrofishing with push nets and dip nets. Single-pass electrofishing catch efficiency was verified through comparison with three-pass electrofishing (with use of a stop-net) in a separate investigation in 2017 to ensure that metrics generated were unbiased (see Appendix 2B). Fish were anesthetized (using AQUI-S^{TM} 20E; AQUI-S New Zealand Ltd.), counted, measured for total length (mm), and identified to species. Six fish of representative taxa and sizes (spanning the smallest, medium, and largest) from each reach were euthanised (if <400 mm TL) with an overdose of AQUI-S and frozen, or a non-lethal fin clip was taken (if >400 mm TL;

Sanderson et al. 2009) and frozen for later stable isotope processing in the laboratory (Post 2002).

Non-lethal fin clips were preferred for extracting SI values from large-bodied Salmonidae spp. and *Anguilla dieffenbachii* because these fishes are long-lived, sensitive species and large individuals are disproportionately important for reproduction, sports fishing and human harvest. A small portion of tissue (1 mg +/- 0.2) was removed from pelvic or pectoral fins of these large fishes with surgical scissors (Hanisch et al. 2010); judicious removal of cartilaginous fin tissue is non-invasive and does not negatively affect adult fish swimming ability or survival (Gjerde & Refstie 1988; Wagner et al. 2009).

Fish mass (wet mass, g) was calculated from field-measured total or fork length (depending on the morphology of the species), using Jellyman et al. (2013a; Figure 2A.2) regressions relating fork length, total length, and mass; a subset of fish euthanized for this study were measured in the field and weighed in the laboratory to verify the accuracy of the published relationships. Fish mass was $\log_2$-transformed for mass–abundance relationships (Jennings et al. 2002) to best fit the spread of the data and binned for each reach, and abundance of each bin (set at a $\log_2$ scale bin width to best fit the range of fish size at my reaches) was also $\log_2$-transformed. A linear regression was constructed relating $\log_2$ binned abundance to the midpoints of $\log_2$-binned fish mass. For each mass–abundance relationship, the slope, mass range, maximum body size, and total fish biomass (all $\log_2$ transformed) were extracted to use as response variables.

Stable isotope preparation and analysis

Primary consumers (*Deleatidium* spp., Leptophlebiidae mayflies) were collected with a kicknet at each stream reach sampled in 2016, and frozen prior to transport back to the laboratory to use as a baseline to compare with fish for SI food-chain length analysis (McHugh et al. 2012). *Deleatidium* spp. were chosen as a baseline consumer because they are

ubiquitous in the stream network, constitute a large percentage of primary consumer biomass in many streams, and are a common dietary item for fishes (McHugh et al. 2010). *Deleatidium* from each reach were dissected and the stomach contents and head removed to eliminate bias (Lancaster & Waldron 2001), and samples were pooled from at least 20 individuals from each reach (Post 2002). Dorsal muscle tissue was dissected from fish samples. Fish and invertebrate tissues were subsequently dried in an oven for at least 72 hours at 50°C. Samples were ground into a fine powder using a mortar and pestle, with care taken to avoid contamination, and approximately 2 mg of powder was placed in tin capsules (8 x 5 mm) and sent to the University of California-Davis Stable Isotope Facility for analysis through isotope ratio mass spectrometry (PDZ Europa 20-20; Sercon Ltd.). Carbon isotope values were corrected for lipid content using established relationships (Post et al. 2007).

Resulting ^{15}N: ^{14}N ($\delta^{15}N$) isotope ratios were used to calculate trophic position of each sample organism (*i*), using the following equation from Post et al. (2000):

$TP_{ij} = \lambda + (\delta^{15}N_{ij} - \delta^{15}Nbase_j) / \Delta$ (Equation 2.1),

where $\delta^{15}Nbase_j$ is the mean baseline from reach *j*, λ is the trophic position of the baseline (primary consumer; 2), and Δ is the mean fractionation rate (3.4‰; Post et al. 2000). Fish TP values from each reach were used to calculate an estimate of food-chain length (FCL) using the equation:

FCL_j = Maximum fish ($\delta^{15}N_{ij}$) – baseline consumer ($\delta^{15}N_j$) (Equation 2.2).

Carbon range (CRange), a measure of dietary breadth of fishes, was calculated for each reach, following the equation:

$CRange_j$ = Maximum ($\delta^{13}C_{ij}$) – minimum ($\delta^{13}C_{ij}$) (Equation 2.3),

for individual fish taxa (*i*) sampled for isotopes within reach *j* (McHugh et al. 2015).

For *S. trutta* and *A. dieffenbachii*, individuals larger than 400 mm had fin clips taken. Fin clip SI values were not corrected to muscle values for *S. trutta* per McCarthy & Waldron (2000), who found no significant differences between tissue types for this species. A regression relating *A. dieffenbachii* fin clips to muscle values was constructed from a subset of euthanized individuals as follows:

$\delta^{13}C_{corrected} = 0.6035 * \delta^{13}C_{fin\ clip} - 10.206$ (Equation 2.4; $R^2 = 0.99$; Figure 2A.3b) and

$\delta^{15}N_{corrected} = 1.0402 * \delta^{15}N_{fin\ clip} - 0.4065$ (Equation 2.5; $R^2 = 0.97$; Figure 2A.3a).

Using Equations 2.4 and 2.5, all *A. dieffenbachii* fin clip SI values were corrected to muscle values for FCL and CRange analysis (Jardine et al. 2005).

Data analysis

I evaluated relationships between various responses, including the slope of fish mass–abundance relationships, mass range, maximum body size, total fish biomass, FCL, and CRange, and predictor variables as outlined in hypotheses. To test *H1* (habitat size effect), discharge, cross-sectional area, wetted width, and average depth predictors were included in models explaining each response. For *H2* (flood-proneness) I included RDI as a variable, which was the only variable that captured flood-proneness (remotely-sensed variables have proven unsuitable, Doug Booker (NIWA) *personal communication*). Remotely-sensed riparian land cover predictors, specifically indigenous forest, tussock, scrub, and bare ground were included to test *H3* (effect of land cover), and for *H4* (effect of predator presence) eel and trout presence were put in models for evaluation. Evaluating *H5* (contribution of variable type and spatial scale) was accomplished by assessing goodness-of-fit of models and noting variable types that most-often appeared in top models. Collinearity of predictors was eliminated by calculating correlation values and variance inflation factors (VIF) and pruning collinear variables ($VIF \geq 4$); VIF cutoff value was conservatively set to the lowest value in

literature (Pan & Jackson 2008), rather than VIF ≥10 used in most studies (Craney & Surles 2002), to ensure predictor independence. A set of generalized linear models was constructed for each response variable separately using 'lmer' in R version 3.4 (Package 'lme4'; R Development Core Team, 2016). Subcatchment was included as a random effect in all models to account for spatial autocorrelation in the stream network (see Table 2A.1).

Candidate models reflecting hypotheses 1–4 were built using an *a priori* approach to predictor selection. These models were based on observed relationships in preliminary data plots which prevented model overfitting and used known factors that fish populations and aquatic communities respond to (Wenger et al. 2008). Models (20–40 for each response variable) were constructed with a combination of predictor types (for different hypotheses; Table 2.2). I used an information-theoretic approach to select the best models predicting body size and trophic metrics (Burnham & Anderson 2002); model selection using Akaike's information criterion (AIC) is considered the best way to approximate true relationships in a multivariate, exploratory, analysis such as ours (Buckland et al. 1997; Jonson & Omland 2004; Symonds & Moussalli 2011). In light of the findings of Jellyman et al. (2014), candidate sets with interaction between discharge and RDI were also tested, but an interaction term was not retained in the final model as there was no reduction in the AIC score.

Model selection was based on AIC scores corrected for small sample size (AICc; Hurvich & Tsai 1989); the top models were those with the lowest AICc (ΔAICc < 2; Burnham & Anderson 2002; Posada & Buckley 2004). Predictors in top models were model–averaged to increase precision and reduce uncertainty (using the 'model.avg' function in R version 3.1.3, package 'MuMiN'; Burnham & Anderson 2002; R Development Core Team 2016; Symonds & Moussalli 2011). Ninety-percent confidence intervals (90% CI) for model–averaged parameters were calculated to evaluate whether parameters overlapped zero (zero-overlap indicates a non-significant effect of a predictor on the response; Buckland et al.

1997). Additionally, marginal R^2 (proportion of variance explained by fixed effects) and conditional R^2 (proportion of variance explained by fixed and random effects) values were calculated for the top model of each response to assess goodness-of-fit (because AICc only ranks models relative to each other; Nakagawa & Schielzeth 2013; Symonds & Moussalli 2011).

Results

Fish community composition

Of 30 stream reaches electrofished in 2016, 29 yielded one or more individual fish for analysis. There were 906 fish captured, identified, and measured (length); tissue was collected from 164 individuals of representative size and species for SI analyses. Historic data from 16 reaches sampled in 1997, 2004, 2005, and 2009 contained species and length measurements for an additional 554 fish (no SI data). Fish capture methods for historic data were comparable to those used in 2016 (i.e., first pass data was extracted from three-pass electrofishing datasets). Fish species collected from all years included Canterbury galaxias (*Galaxias vulgaris*), alpine galaxias (*Galaxias paucispondylus*), koaro (*Galaxias brevipinnis*), upland bully (*Gobiomorphus breviceps*), *A. dieffenbachii*, *O. mykiss*, *O. tshawytscha*, and *S. trutta*.

Species richness varied among reaches from one to five taxa, and incorporated native and non-native species, although not always co-occurring. *Salmo trutta* (present at 34 of 46 reaches) and *G. vulgaris* (26 reaches) were most ubiquitous, while *G. brevipinnis* (2 reaches) and *O. tshawytscha* (7 reaches) were least widespread. Across sampling reaches, *G. vulgaris* (31.3% of total catch) and *S. trutta* (22.6%) were the most abundant taxa, and the most uncommon were *G. brevipinnis* (1.6%) and *A. dieffenbachii* (4.1%). *Anguilla dieffenbachii* (42.6%) and *S. trutta* (36.0%) dominated total fish biomass across all reaches, with *O.*

tshawytscha (0.7%) and *G. brevipinnis* (0.5%) contributing the least. Mean fish body sizes from all data were 86.4 mm for length (SE ± 2.2) and 11.7 g (SE ± 1.9) for mass.

Published regressions relating fish fork length, total length, and wet weight closely fit the subset of fish I measured in the field and weighed in the laboratory (n = 434 individuals from this study and previous investigations; $R^2 > 0.96$ across all species, Figure 2A.2). Mass–abundance relationships with fewer than five data points (e.g., reaches 'BRK' and 'LHR' in Figure 2A.4) were excluded from the slope response analysis because robust slope and goodness-of-fit values could not be calculated. However, I could not calculate mass range, maximum body size, and food-chain length for these low-abundance reaches. Of the 46 reaches sampled in all years, 41 had enough data points to be included in the mass–abundance relationship analysis. The slope values for all 41 mass–abundance relationships ranged from -0.38 to -1.77 (mean = -1.11). Among reaches, mass range averaged 146.8 (g; SE +/- 54.3), maximum body size had a mean of 149.7 (g; SE +/- 54.3), and total fish biomass averaged 372.8 (g; SE +/- 75.3). Food-chain length and carbon range were calculated for 29 of the stream reaches (from n = 164 fish). Across reaches, FCL averaged 3.53 (SE +/- 0.14), while CRange had a mean of 2.64 (SE +/- 0.44).

*Habitat size effects (*H1*)*

Top models for only mass–abundance slope and food-chain length included the habitat size (FLO; discharge; Tables 2.3 and 2.5) variable. The confidence interval for FLO overlapped zero when model–averaged for mass–abundance, and thus was not deemed a significant predictor (Table 2.4). However, stream reaches with higher discharge had longer food chains (Table 2.6; Figure 2.4), indicating increased habitat size leads to more trophic links in the aquatic community.

*Flood-proneness (*H2*)*

Similar to habitat size, RDI was only included in top models for mass–abundance slope and carbon range (Tables 2.3 and 2.5). Model-averaging indicated that increasing RDI resulted in a significant decrease in mass–abundance slope and carbon range (Tables 2.4 and 2.6). Therefore, increased flood-proneness and decreased stability resulted in a steepening of mass–abundance slope (Figure 2.2). This was due to loss of large-bodied size classes of fish and an increase in abundance of small-bodied size classes, resulting in a shift in the mass–abundance relationship. In the case of carbon range, increased flood-proneness resulted in a narrowing of dietary breadth for fishes (Figure 2.5).

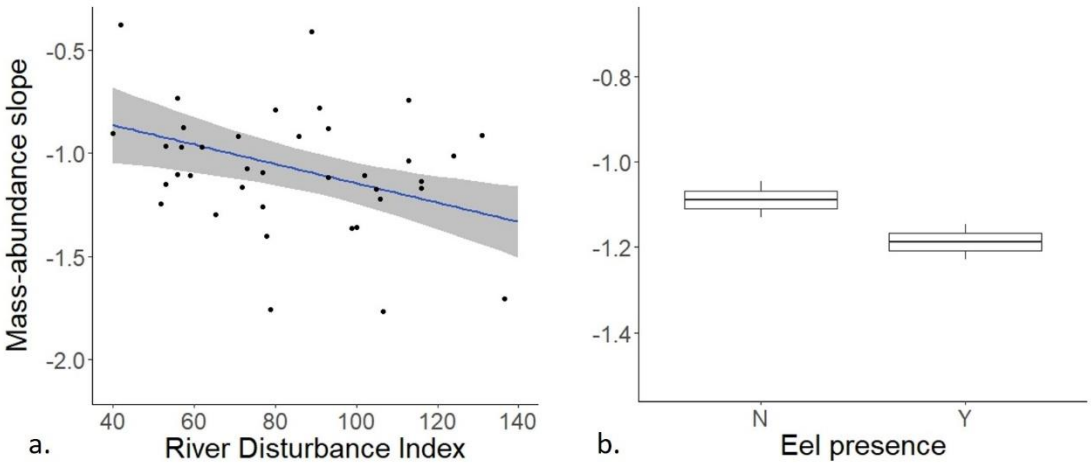

Figure 2.2. Predicted effects (with other variables held at average values) of (a) flood proneness (river disturbance index [RDI]; unitless) and (b) eel presence (N = absent, Y = present) on fish mass–abundance relationship slope. Increasing RDI equates to higher flood proneness. Boxes represent the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, and solid lines the median. The shaded ribbon is based on parameter 90% confidence limits as listed in Table 2.3.

Table 2.3. Summary of model selection statistics for top models (ΔAICc < 2) predicting fish body size, abundance, and biomass metrics in the Waimakariri River catchment, New Zealand. Fine-scale variables are denoted by 'S' and large-scale variables are denoted by 'L' in the scale column. Variable type is 'F' for field-measured abiotic,'B' for field measured biotic, and 'R' for remotely-sensed abiotic. Models with a combination of types or scales are indicated by 'C.' Abbreviations are as follows: L-L = the log-likelihood; ΔAICc= the difference in the corrected Akaike information criterion (AICc) value for a particular model compared with the top-ranked model; w_i = the AICc weight, E_r = the evidence ratio (i.e., w_{top}/w_i); K = the number of parameters, including the intercept and residual variance; mR^2 = the marginal R^2 of the top model; and cR^2 = the conditional R^2 of the top model.

Response	Model	Type	Scale	L-L	AICc	ΔAICc	w_i	E_r	K	mR^2	cR^2
Mass–abundance slope	RDI	F	S	-10.52	30.14	0.00	0.17	1.0	4	0.17	0.17
	RDI, EEL	C	S	-9.25	30.21	0.07	0.16	1.1	5	0.22	0.22
	RDI, EEL, segTussock	C	C	-7.89	30.26	0.12	0.16	1.1	6	0.27	0.27
	RDI, segTussock	C	C	-9.96	31.64	1.49	0.08	2.1	5	0.19	0.19
	RDI, FLO	F	S	-10.04	31.80	1.65	0.07	2.4	5	0.19	0.19
Mass range (Log_2 g)	EEL, TROUT, segTussock	C	C	-99.02	212.20	0.00	0.37	1.0	6	0.47	0.47
	EEL, TROUT, segTussock, usIndigForest	C	C	-98.17	213.29	1.09	0.21	1.8	7	0.49	0.49
Maximum size (Log_2 g)	EEL, TROUT, segBare	C	C	-81.74	177.63	0.00	0.57	1.0	6	0.60	0.60
	EEL, TROUT	B	S	-84.04	179.58	1.95	0.21	2.7	5	0.56	0.60
Total biomass (Log_2 g)	EEL, segBare	C	C	-63.65	139.00	0.00	0.28	1.0	5	0.44	0.44
	EEL, segBare, usIndigForest	C	C	-62.48	139.43	0.42	0.23	1.2	6	0.47	0.47

*Riparian land cover (*H3*)*

Riparian land cover variables were present in top models for all responses. Percent tussock cover was included in top models for mass–abundance slope, mass range, food-chain length, and carbon range (Tables 2.3 and 2.5). Tussock cover was correlated with a significant increase in fish mass range and carbon range of fish diets (Tables 2.4 and 2.6, Figures 2.3 and 2.5). Thus, streams flowing through tussock land were more likely to have a

wider range of fish sizes and increased dietary breadth. Similarly, upstream indigenous forest cover was present in top models for fish mass range and community food-chain length. While the confidence interval for usIndigForest overlapped zero for mass range, indigenous forest was found to significantly affect food-chain length (Table 2.6). Specifically, streams with more upstream native bush had longer food-chain lengths (Figure 2.4), indicating an increase in trophic linkages. Contrastingly, percent of bare ground cover was included in top models for maximum fish size and total fish biomass (Table 2.3), but was found to be significant only for biomass (Table 2.4). In this case, increased bare ground cover resulted in less fish biomass within a reach (Figure 2.3h). Finally, riparian scrub was present in top models for only food-chain length and carbon range (Table 2.3), and significantly affected both of these responses (Table 2.5). Specifically, increased scrub was associated with streams with longer food-chain lengths (Figure 2.4) but decreased dietary breadth for fishes (Figure 2.5).

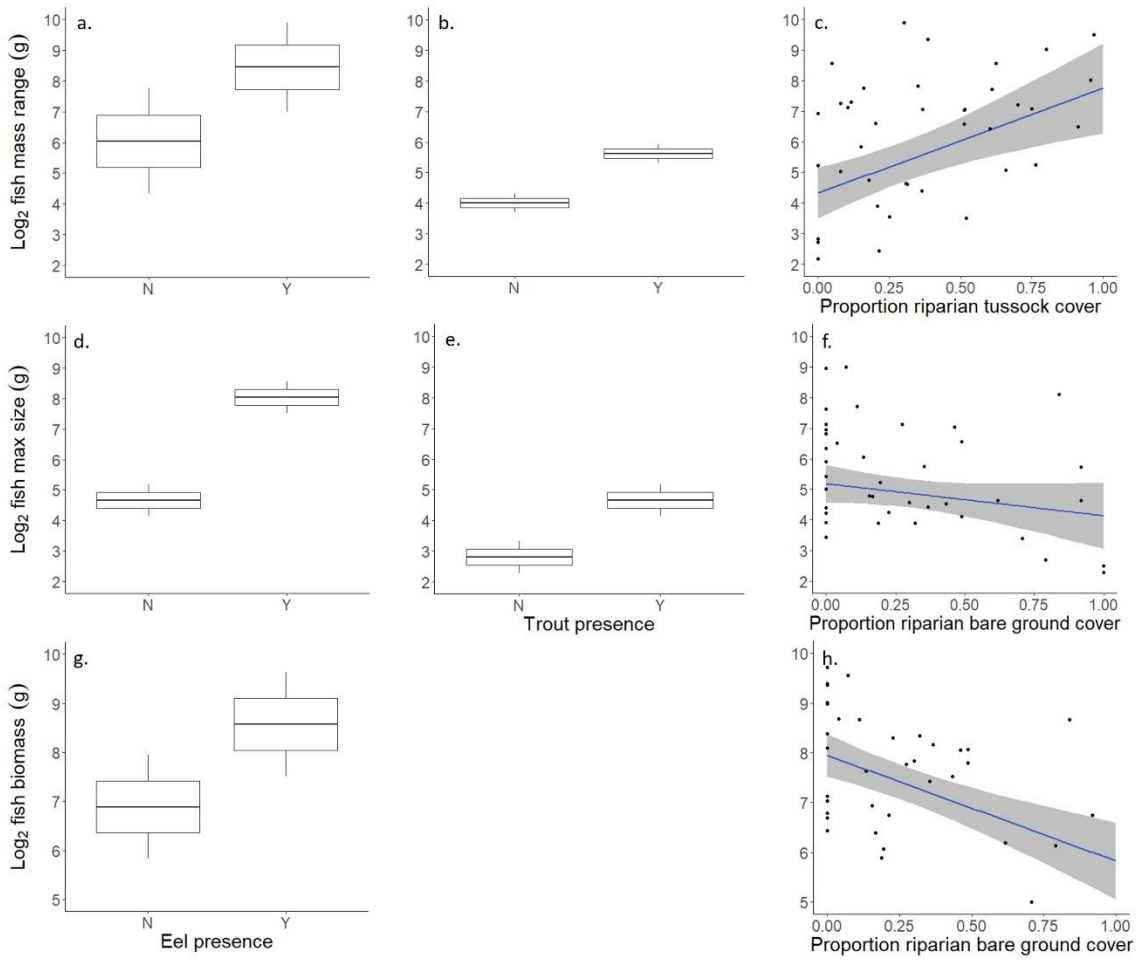

Figure 2.3. Predicted effects (with other variables held at average values) of (a) eel presence (N = absent, Y = present), (b) trout presence and (c) proportion riparian tussock cover on $\log_2$ fish mass range (grams); effect of (d) eel presence, (e) trout presence and (f) proportion riparian bare ground cover on $\log_2$ maximum fish body size (grams); and effects of (g) eel presence and (h) proportion riparian bare ground cover on $\log_2$ fish biomass (grams). Boxes represent the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, and solid lines the median. The shaded ribbons are based on parameter 90% confidence limits as listed in Table 2.3

*Effects of predator presence (*H4*)*

Top models for all responses (Tables 2.3 and 2.5) and model-averaging (Tables 2.4 and 2.6) showed that the presence of native longfin eels significantly affected fish body size and food-web metrics (90% CI for the EEL model parameter did not overlap zero). Eel presence caused mass–abundance slopes to significantly steepen, indicating that rivers with eels had fish assemblages where abundance declined comparatively more steeply with fish body size (Figure 2.2b). Additionally, the presence of these large-bodied predators correlated with an increase in fish mass range, maximum size, and biomass in stream reaches (Figure

2.3). Similarly for food web metrics, eels were associated with longer food-chain lengths (Figure 2.4) and greater carbon range (Figure 2.5) within fish diets. Unlike eels, the presence of predatory non-native trout did not influence fish body size or food-web metrics as strongly. Trout presence was only included in top models for fish mass range and maximum body size (Table 2.3), and was associated with an increase in these metrics only (Figure 2.3).

Table 2.4. Model–averaged parameter estimates, Z-statistic probability value (Pr(>|z|)), relative variable importance (Ri), and unconditional SE values (in parentheses) and lower and upper 90% confidence limits (CLs) for covariates (Table 2.3) predicting fish body size, abundance, and biomass metrics for reaches in the Waimakariri River catchment, New Zealand. Estimates are derived from averaging of models with ΔAICc < 2.

Response	Covariate	Parameter estimate (SE)	Pr(>|z|)	R_i	Lower 90% CL	Upper 90% CL
Mass–abundance slope	RDI	-0.01 (0.01)	0.01	1.00	-0.008	-0.01
	EEL	-0.20 (0.11)	0.08	0.50	-0.384	-0.01
	segTussock	0.26 (0.18)	0.17	0.37	-0.050	0.57
	FLO	-0.06 (0.06)	0.34	0.11	-0.154	0.04
Mass range (Log_2 g)	EEL	2.66 (0.76)	<0.01	1.00	1.393	3.94
	segTussock	3.42 (1.10)	<0.01	1.00	1.561	5.28
	TROUT	1.61 (0.73)	0.03	1.00	0.382	2.84
	usIndigFores	1.64 (1.24)	0.20	0.37	-0.455	3.73
Maximum size (Log_2 g)	EEL	3.37 (0.49)	<0.01	1.00	2.55	4.20
	TROUT	1.86 (0.51)	<0.01	1.00	1.00	2.72
	segBare	-1.44 (0.63)	0.03	0.73	-2.51	-0.37
Total biomass (Log_2 g)	EEL	1.68 (0.39)	<0.01	1.00	1.02	2.34
	segBare	-2.12 (0.57)	<0.01	1.00	-3.08	-1.16
	usIndigFores	1.05 (0.68)	0.13	0.45	-0.09	2.19

*Model performance, variable types, and spatial scales (*H5*)*

Overall, conditional R^2 (cR^2) for the top model from each set was moderate for most responses ($0.44 < cR^2 < 0.72$), indicating intermediate explanatory power for these variables (Table 2.3 and Table 2.5). Notably, explanatory power was poor for the top model explaining mass–abundance slope ($cR^2 = 0.17$). Models including a combination of abiotic (FLO, RDI,

segScrub, usIndigForest, segTussock) and biotic (EEL and TROUT) predictors dominated the top model sets for stable isotope-derived responses (included in 88% of top models; Table 2.5), with only a single local biotic-only (EEL) model present in this group. Similarly for spatial scale model composition, a combination of variables reflecting processes at different scales was seen in all models except for one local-scale-only model.

Table 2.5. Model selection statistics for top mixed effect-models for covariates (Table 2.1) predicting food-chain length ($\Delta\delta^{15}N_{max}$ - $\Delta\delta^{15}N_{min}$) and carbon range ($\Delta\delta^{13}C_{max}$ - $\Delta\delta^{13}C_{min}$) in the Waimakariri River catchment, New Zealand. (ΔAICc < 2). Fine-scale variables are denoted by 'S' and large-scale variables are denoted by 'L' in the spatial scale column. Variable type is 'F' for field-measured abiotic, 'B' for field measured biotic, and 'R' for remotely-sensed abiotic. Models with a combination of types or scales are indicated by 'C.' Abbreviations are as follows: L-L = the log-likelihood; ΔAICc= the difference in the corrected Akaike information criterion (AICc) value for a particular model compared with the top-ranked model; w_i = the AICc weight, E_r = the evidence ratio (i.e., w_{top}/w_i); K = the number of parameters, including the intercept and residual variance; mR^2 = the marginal R^2 of the top model; and cR^2 = the conditional R^2 of the top model.

Response	Model	Type	Scale	L-L	AICc	ΔAICc	w_i	E_r	*K*	mR^2	cR^2
Food-chain length	EEL, FLO, segScrub, usIndigForest	C	C	-4.54	28.42	0	0.19	1.00	7	0.51	0.51
	EEL	B	S	-9.74	29.14	0.72	0.13	1.46	4	0.26	0.44
	EEL, segScrub, usIndigForest	C	C	-6.74	29.31	0.88	0.12	1.58	6	0.43	0.45
	EEL, segScrub	C	C	-8.84	30.29	1.87	0.07	2.71	5	0.33	0.41
	EEL, segTussock	C	C	-8.88	30.37	1.95	0.07	2.71	5	0.30	0.45
Carbon range	EEL, segTussock	C	C	-53.65	119.90	0	0.25	1.00	5	0.53	0.72
	EEL, segScrub, RDI	C	C	-52.13	120.07	0.17	0.23	1.09	6	0.51	0.77
	EEL, segTussock, segScrub	C	C	-51.13	121.58	1.68	0.12	2.08	7	0.55	0.73

Most top models for mass–abundance and body size responses included combinations of predictor types (local biotic, local abiotic, and remotely-sensed abiotic; 73% of top models; Table 2.3), but non-combination models with local abiotic (18%) and biotic (9%)

variables only also appeared. Here, top models for mass range only included combinations, but maximum body size models included a model with biotic-only variables. There were no models containing only remotely-sensed abiotic predictors in the top sets for any response variable. Similarly, for spatial scale, models with variables of combined scale (both field-measured 50 m and FWENZ 740 m) dominated (64%), while there were fewer models with only local-scale predictors (36%) and no models that contained only broad-scale FWENZ variables.

Table 2.6. Model–averaged parameter estimates, Z-statistic probability value (Pr(>|z|)), relative variable importance (Ri), and unconditional SE values (in parentheses) and lower and upper 90% confidence limits (CLs) for covariates (Table 2.5) predicting food-chain length ($\Delta\delta^{15}N_{max}$ - $\Delta\delta^{15}N_{min}$) and carbon range ($\Delta\delta^{13}C_{max}$ - $\Delta\delta^{13}C_{min}$) in the Waimakariri River catchment, New Zealand. Estimates are derived from confidences set of models with ΔAICc < 2.

Response	**Covariate**	**Parameter Estimate (SE)**	**Pr(>|z|)**	**R_i**	**Lower 90% CL**	**Upper 90% CL**
Food-chain length	EEL	0.53 (0.14)	<0.01	1.00	0.29	0.77
	segScrub	0.65 (0.30)	0.04	0.65	0.14	1.15
	usIndigForest	0.57 (0.23)	0.02	0.53	0.17	0.96
	FLO	0.12 (0.05)	0.04	0.32	0.03	0.21
	segTussock	-0.27 (0.20)	0.20	0.12	-0.62	0.08
Carbon range	EEL	2.63 (0.67)	<0.01	1.00	1.62	3.77
	segTussock	2.49 (1.07)	0.03	0.61	0.49	4.38
	RDI	-0.03 (0.01)	0.05	0.57	-0.04	-0.01
	segScrub	-3.28 (1.67)	0.06	0.57	-6.26	-1.56

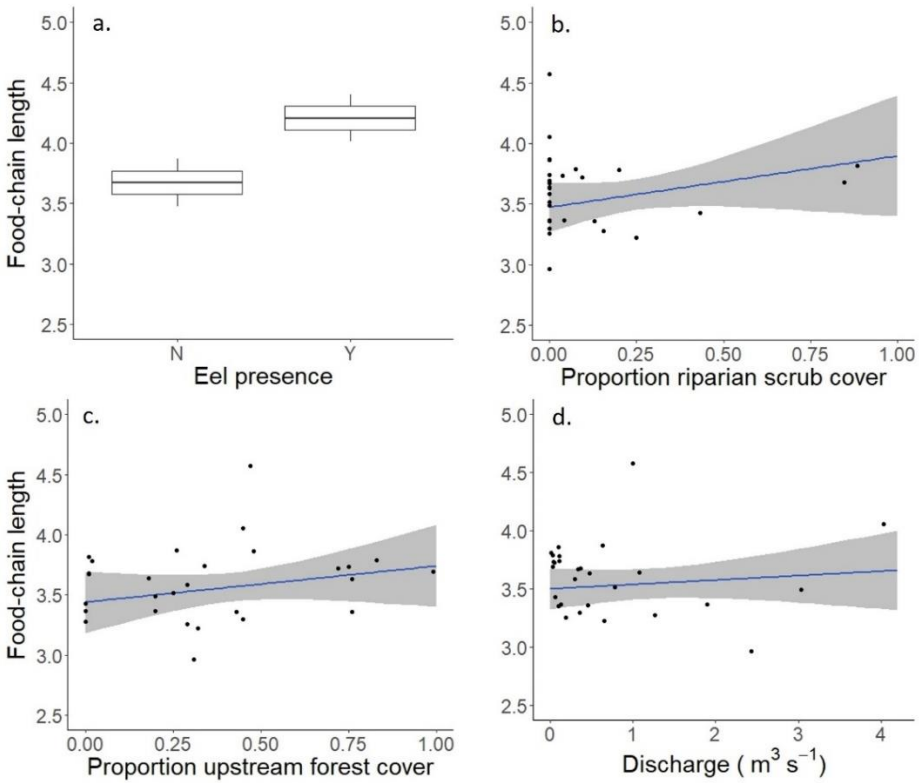

Figure 2.4. Predicted effects (with other variables held at average values) of (a) eel presence (N = absent, Y = present), (b) proportion riparian scrub cover, (c) proportion upstream indigenous forest cover and (d) discharge (m^3/s) on food-chain length ($\Delta\delta^{15}N_{max} - \Delta\delta^{15}N_{min}$). Shaded ribbons are based on parameter 90% confidence limits as listed in Table 2.5.

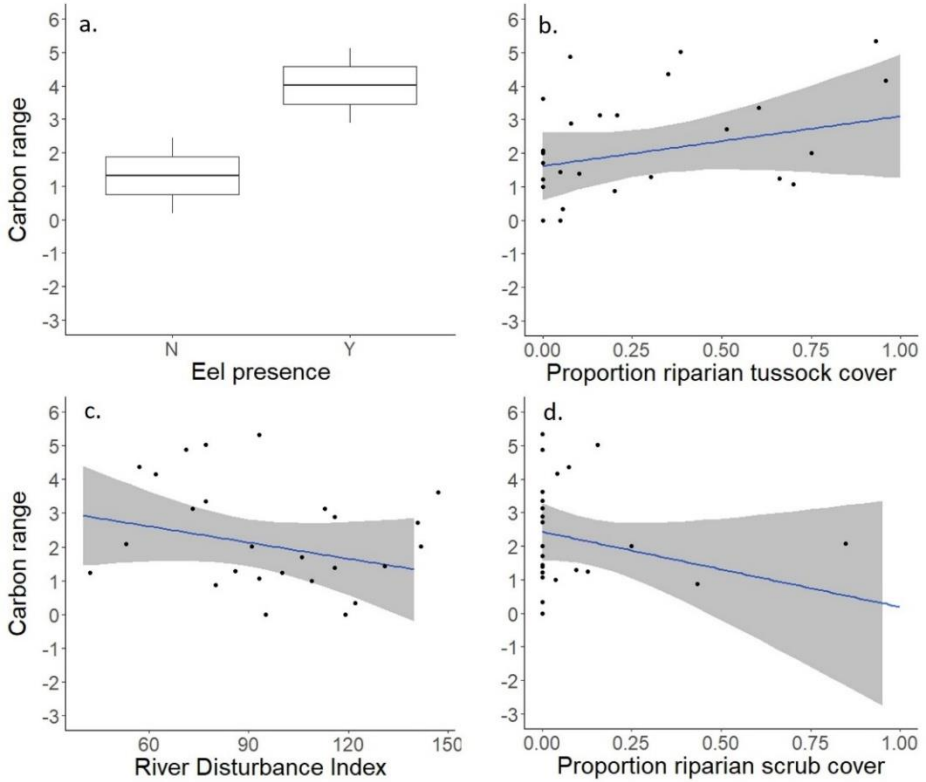

Figure 2.5. Predicted effects (with other variables held at average values) of (a) eel presence (N = absent, Y = present), (b) proportion riparian tussock cover, (c) river disturbance index and (d) proportion riparian scrub cover on carbon range ($\Delta\delta^{13}C_{max} - \Delta\delta^{13}C_{min}$) in stream reaches. Shaded ribbons are based on parameter 90% confidence limits as listed in Table 2.5.

Discussion

Given that characterisation of food webs is useful for summarizing energy flow in freshwaters but is often time-consuming and impractical to apply at a broad extent, proxy metrics provide a more feasible way to encapsulate trophic patterns (Arim et al. 2010). My study reinforced this, finding that mass–abundance relationships of fish assemblages and stable isotope-derived metrics may provide useful, complementary methods for quantifying functional measures of community structure (Sterner et al. 1997; Post et al. 2002) in rivers across a range of sizes and flow regimes. Additionally, some of these metrics responded as hypothesized to habitat factors at multiple spatial scales and to both biotic and abiotic factors, highlighting the importance of incorporating local and landscape influences of varying resolution in lotic food-web analyses (which should be accounted for when using these metrics). The usefulness of these methods could lead to application in other freshwater systems, in New Zealand or internationally, to characterise fish-centric aquatic food webs and identify factors that affect them. Specific applications could include before-and-after research around human development that may affect freshwater ecosystems, or monitoring of food-web or fish assemblage changes in ecosystems with particularly sensitive or endangered taxa to quickly identify and take action in response to perturbations.

*Habitat size (*H1*)*

First I examined the effects of stream discharge (as a proxy for habitat size), which was not influential for fish body size metrics as I expected, but reliably predicted an SI-derived measure (food-chain length). The lengthening of food chains with increased discharge was expected, because larger streams have more available space, a greater opportunity for habitat heterogeneity and potentially more food resources to support additional predatory fish species (Ziegler et al. 2017). Increases in fish body size in larger habitats were expected to be an important driver of increasing food-chain length (McHugh et

al. 2010), so it was unexpected that fish body size did not respond similarly. The discrepancy may be due to discharge being an imperfect estimate of habitat size, or alternatively the composition of fish assemblages across reaches, because different fishes (e.g., trout vs. eels) have different body shapes, metabolic rates, maximum sizes, and life histories (Gaye-Siessegger et al. 2004; Gillooly et al. 2001). Other studies of habitat size effects similarly found clear effects on aquatic food-chain length, particularly when RDI was factored in (McHugh et al. 2010; McHugh et al. 2015). However, unlike Jellyman et al. (2014), I did not find evidence that habitat size affected fish body size, likely due to the propensity for large-bodied *Anguilla dieffenbachii* to occasionally occupy very small streams with undercut banks or tree-root microhabitats (Glova et al. 1998; McHugh et al. 2010; K. Fraley *personal observations*). Thus, habitat size can be considered an important driver of trophic structure in streams, but may be confounded by the presence of mobile, large-bodied predators in small habitats.

*Flood-proneness (*H2*)*

In a contrast to the effects of habitat size, flood-proneness was correlated to both trophic metrics and mass–abundance relationships. Increasing flood disturbance steepened mass–abundance relationships, indicating that there were more small-bodied fishes present in flood-prone reaches relative to large-bodied ones. This is likely because flood disturbance is closely linked to productivity (Death & Zimmerman 2005), and more flood-prone reaches would be expected to contain fewer food resources (lower standing stock of algae and thus invertebrate prey) of a lower diversity and lack intermediate consumers when compared to less-disturbed reaches where primary production is not constantly reset (Biggs 1995; Matthaei et al. 1999). Dietary breadth was also negatively affected by flood-proneness and similar mechanisms (e.g., a lower diversity of prey items) coupled with less allochthonous inputs because of lack of riparian vegetation in hydrologically-disturbed reaches may

partially explain this result. Unlike the findings of McHugh et al. (2010), but similar to Townsend et al. (1998), RDI did not affect the food-chain length. This may be due to the occasional presence of very large, relatively mobile taxa in reaches with high flood disturbance. Thus, the scales at which different fish taxa move and travel within, as well as their transience, are likely very important in modulating the structure of freshwater food webs (Fausch et al. 2002). Alternatively, this discrepancy could be due to increased piscivory (thus increasing the upper trophic level and FCL) in fishes inhabiting harsher, flood-prone reaches.

*Riparian land cover (*H3*)*

Similar to what was detected with flood-proneness, both fish body size and stable isotope metrics responded significantly to land-cover variables as expected. Upstream native forest cover boosted food-chain length, indicating the potential importance of intact forest for the stability of aquatic food webs. This link could occur directly or indirectly through terrestrial food subsidies (i.e., increased input of detritus, spiders, native bush cockroaches, and even mice; Baxter et al. 2005; Lisi et al. 2014). Riparian scrub cover was correlated with increased food-chain length, perhaps due to allochthonous inputs similar to those of indigenous forest cover (Joy & Death 2004; Rounick et al. 1982). Increased percentage of riparian area covered by tussock grasses boosted fish mass range as well as carbon range, which is in-line with findings of Edwards & Huryn (1996), who found that terrestrial invertebrate drift was significantly higher in tussock and forest-cover streams compared to pastureland. This is consistent with reaches with more bare ground riparian cover being correlated with reduced maximum fish size and total fish biomass, likely due to a lower abundance of terrestrial and aquatic insect prey because of reduced habitat along stream margins (Baxter et al. 2005). Thus, the riparian land cover type present along streams is highly influential in determining the sources and flow of energy through the food web.

*Predator presence (*H4*)*

The presence of eels was a key factor in determining fish body-size metrics and stable-isotope metrics, and occurred in the top models of every response. This illustrates the importance of these long-lived, native fish in structuring fish assemblages and their position atop the freshwater trophic pyramid as an important apex predator (Libralato et al. 2006; Mills et al. 1993). While trout (also often large-bodied and predatory) similarly affected several fish body-size metrics, their presence did not modulate mass–abundance slope or isotope values, indicating that they do not add to complexity of fish assemblages and trophic relationships like eels do (Gozlan et al. 2010). This may be due to imperfect adaptation to New Zealand stream environments, given that trout were introduced to New Zealand and established only 150 years ago. Supporting this, trout have been shown to respond negatively to extreme hydrological disturbances (i.e., flooding and drying), which are characteristic of many South Island, New Zealand rivers, while native fishes may persist (Leprieur et al. 2006). Therefore, trout presence may not strongly affect trophic structure, despite the reputation of trout as a predator that decimates native fishes in New Zealand (McIntosh 2000).

*Variable types and spatial scale (*H5*)*

With regard to variable types (abiotic and biotic) and the differential effects of habitat variables measured at specific scales, model selection results illustrated that a combination of local abiotic, local biotic (eel and trout presence), and remotely-sensed abiotic habitat characteristics were the strongest drivers of patterns in fish mass–abundance and body size as well as FCL and CRange. Abiotic and biotic variables measured at the local scale appeared to better-explain relationships between habitat characteristics and responses than remotely-sensed habitat factors measured at a broader scale because there were no models including only remotely-sensed predictors in the top sets, similar to findings of Lammert & Allan

(1999). This partially supports my prediction that abiotic variables measured at the local scale would be the strongest drivers, although species composition (captured by biotic variables), particularly the presence of large-bodied piscivorous species, is also very important in structuring fish assemblages and aquatic communities (Jackson et al. 2001).

In terms of spatial scale, fish and community metrics were also best-explained by variables measured at a combination of different scales, although local-scale (50 m) characteristics appear to be more important (or are sampled at resolution that provides more accuracy) than broad-scale (740 m) remotely-sensed factors. My findings parallel those of Poizat & Pont (1996) and Fraley et al. (2018), who found that the spatial scale of habitats variably affected fishes. The differential effects of habitat at varying spatial scales are likely linked to the mobility and home ranges of the fish species present, thus assemblages with mixed sedentary (e.g., *Gobiomorphus* sp.) and highly mobile (e.g., Salmonidae) fishes that are typical of the study catchment would show responses to variables at both small and large spatial scales. Additionally, the accuracy of remotely-sensed broad-scale variables may not be as high as the directly measured local-scale predictors due to measurement error and aggregation of values, which could have affected my model selection. Therefore, it is important to take into account multiple spatial scales when assessing the effects of habitat on fish assemblages, as well as the error that may be present in broad-scale variables.

Implications and recommendations

The patterns I found illustrate that fish mass–abundance relationships and SI-derived trophic metrics (while only a subset of aquatic food webs) are useful because they summarize trophic processes and functions, and because they respond to various factors influencing freshwater food webs, albeit in different manners. Despite these differences, these methods may be very useful as a complementary, tandem approach to characterising and understanding fish assemblages and aquatic communities (as found in the case of North

Atlantic Ocean fishes; Jennings et al. 2002). This is particularly true when comparing the effort and cost of using these proxies to traditional, intensive food-web quantification methods, as noted by Layman et al. (2005). While land cover, discharge, flood disturbance, and species composition factors significantly affect fish mass–abundance relationships, fish body size, and trophic metrics, they may not be robust enough in my analysis to use in a predictive manner, due to low power to explain variance. (all $R^2 \leq 0.6$). However, if these relationships are examined at a broader scale (i.e, larger than a within-catchment study area) it may be possible to develop predictive models for aquatic food webs and fish assemblages. Thus, mass–abundance and SI-derived trophic measurements could be useful, cost-effective, and time-conserving methods that could be employed by future investigations aiming to characterise and monitor aquatic ecosystems.

Appendix 2A: Supplemental Table and Figures

Table 2A.1. Listing of sampling years, stream reaches, and associated subcatchments in the Waimakariri River catchment, New Zealand. Coordinates are in the WGS84 datum. *Stand-alone streams denote small streams that flowed into the mainstem Waimakariri River, and were considered as a separate subcatchment.

Subcatchment	Reach	Latitude	Longitude	Order	Year
Bealey River	Bealey River at gorge bridge	-42.9168	171.5600	2	2016
	Bealy River at McGrath	-42.9289	171.5600	3	2016
	Edwards River	-42.9738	171.6000	4	2016
	Bealy River braid at Klondike	-43.0057	171.6000	5	2016
Waimakariri River mainstem	Braid near Waimakariri Spring	-43.0168	171.8100	6	2016
	Braid across from Waimak Spring	-43.0183	171.8000	6	2016
	Braid at railroad bridge	-43.0153	171.7100	5	2016
	Braid across from Turkey Flat	-43.0106	171.5700	4	2016
	Braid near Mt. White	-43.0044	171.7546	1	2004
Broken River	Broken River	-43.1934	171.7300	4	2016
	Porter River	-43.2448	171.7300	4	2016
	Cave Stream (Lyndon Saddle)	-43.1485	171.7100	1	2016
	Cave Stream (Flock Hill)	-43.1640	171.7300	2	2016
	Slip Spring	-43.2615	171.7100	2	2016
	Dry Stream	-43.2605	171.7200	2	2016
	Bradley Stream	-43.1901	171.7116	2	2005
	Flock Hill Stream	-43.1681	171.7415	1	2005
	Flock Hill Stream tributary	-43.1732	171.7513	2	2005
	Ghost Stream	-43.2383	171.7423	3	2005
	Roadmarker Stream	-43.2459	171.7238	2	2005
	Whitewater stream	-43.2437	171.7237	3	2009
	Thomas River	-43.2053	171.7071	2	2005
Cass River	Cass River	-43.0260	171.7500	4	2016
	Grasmere Stream site 5	-43.0328	171.7600	4	2016
	Cass Spring	-43.0269	171.7499	4	1997
	Corner Knob	-43.0286	171.7445	2	2004
	Misery Swamp	-43.0376	171.7292	2	1997
Kowai River	Kowai River	-43.3090	171.7700	4	2016
	Coach Stream	-43.3069	171.7600	2	2016
Andrews Stream	Andrews Stream (lower)	-42.9937	171.7900	4	2016
	Peacock Stream	-42.9933	171.7900	2	2016
	Andrews Stream (upper)	-42.9904	171.8000	4	2016
Hawdon River	Hawdon River (upper)	-42.9852	171.7500	4	2016
	Hawdon River (lower)	-42.9954	171.7400	4	2016
Lake Pearson tributaries	Craigieburn Stream	-43.1398	171.7483	3	1997
	Craigieburn Cutting Stream	-43.1407	171.7494	2	2004
	Mansons Creek	-43.1318	171.7663	2	2004

Subcatchment	Reach	Latitude	Longitude	Order	Year
Stand-alone streams*	Lower Farm Stream	-43.0012	171.8100	3	2016
	Binser Stream	-43.0044	171.8100	3	2016
	Cora Lynn Spring	-43.0268	171.6900	3	2016
	Poulter River braid	-43.0382	171.9000	6	2016
	Waimakariri Spring	-43.0162	171.8100	1	2016
	Klondike Spring	-43.0142	171.5900	2	2016
	Turkey Flat Spring	-43.0190	171.5700	1	2016
	Bruce Stream	-43.0283	171.6326	3	2004
	One Tree Swamp	-42.9995	171.7283	2	2004

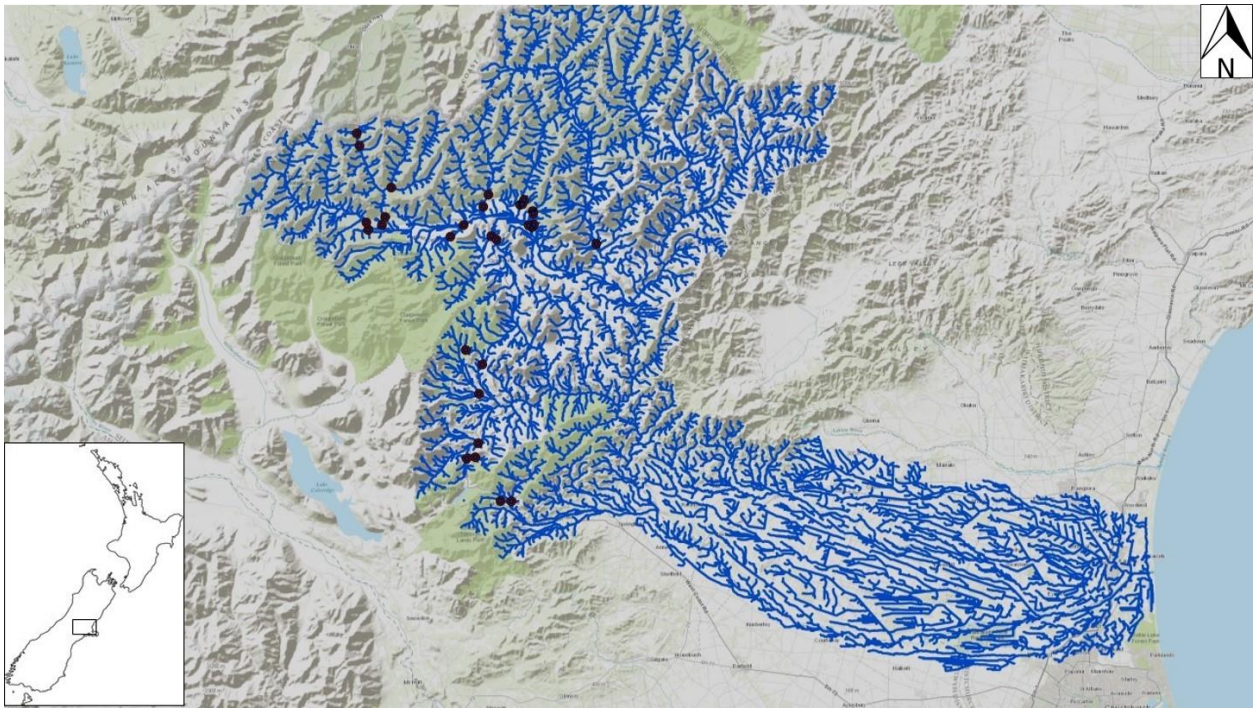

Figure 2A.1. Map of the Waimakariri River catchment in Canterbury, South Island, New Zealand (inset). Blue lines denote tributaries and red dots denote stream reaches sampled for this study.

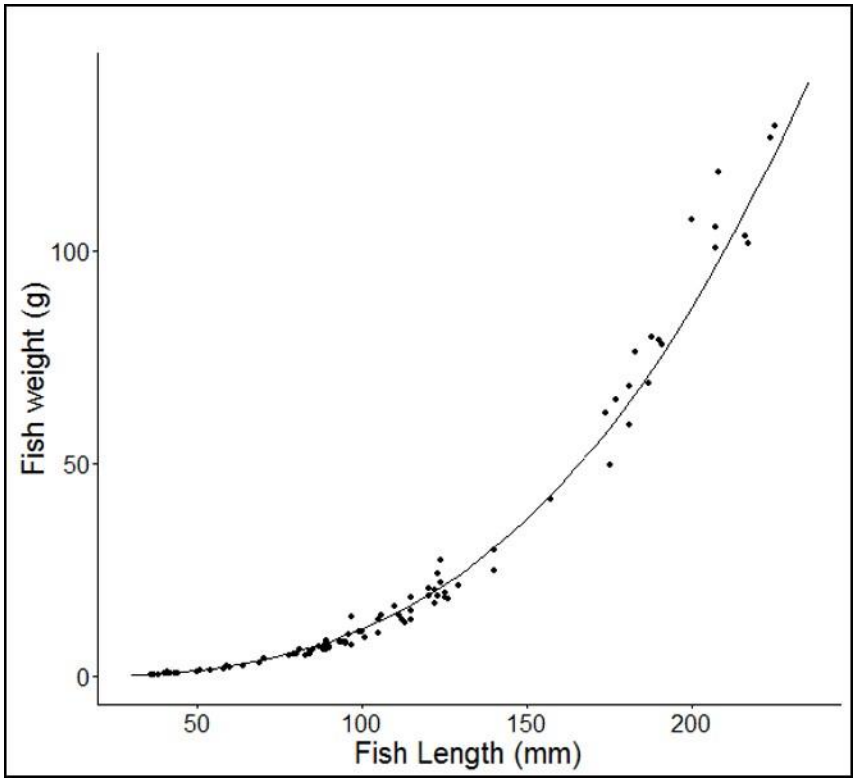

Figure 2A.2. Example of length-weight regression fit for a subset of field-collected and measured fish (*S. trutta*). These regressions were evaluated for all species sampled, and closely fit relationships published by Jellyman et al. (2013; $R^2 > 0.96$).

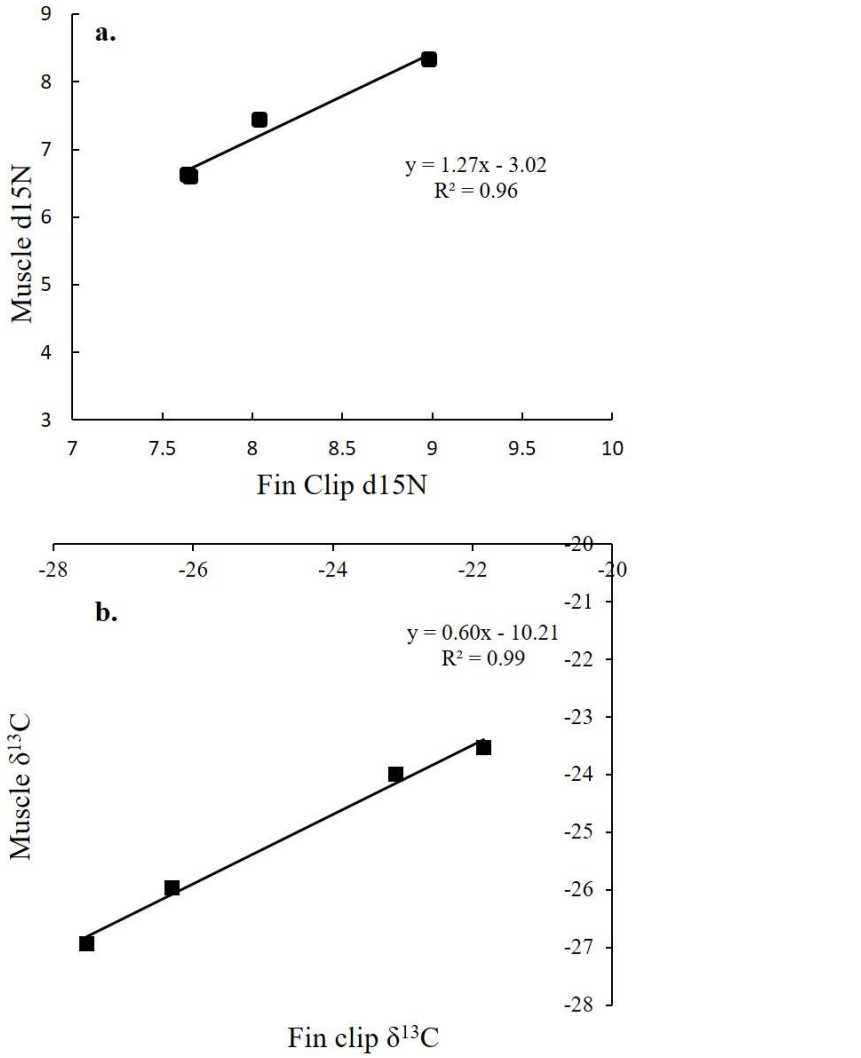

Figure 2A.3. Fin clip to muscle $\delta^{15}N$ (a) and $\delta^{13}C$ (b) correction regressions for *A. dieffenbachii* used to construct Equations 2.4 and 2.5.

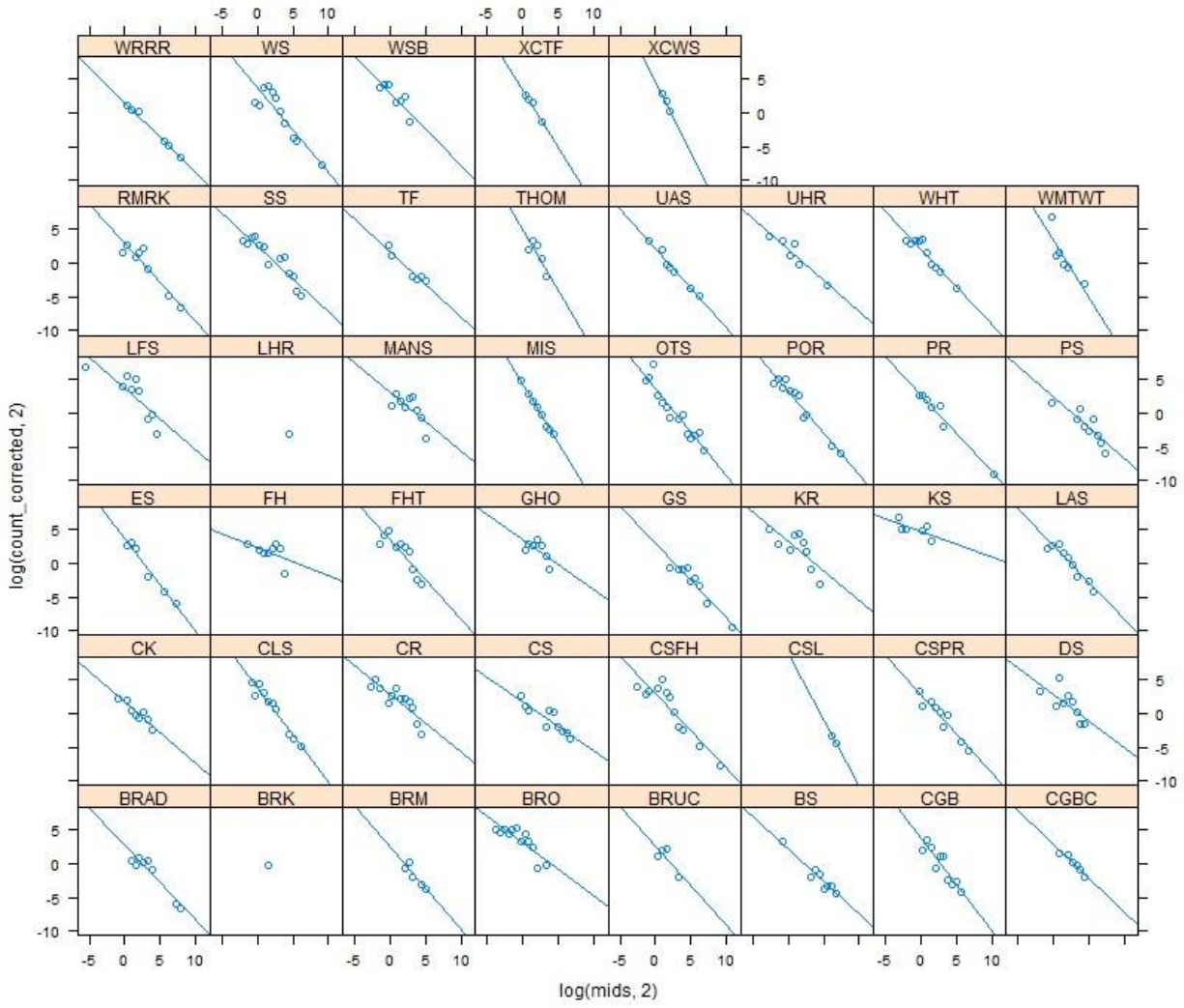

Figure 2A.4. Linear regressions for mass–abundance relationships from sampling reaches in the Waimakariri River, New Zealand. Each graph denotes a sampling reach. Binned mass and abundance are $\log_2$ transformed following Jennings et al. (2002). Mass–abundance relationships (e.g., 'BRK' and 'LHR' in the figure) with fewer than five data points were excluded from analysis

Appendix 2B: Single-pass electrofishing methods verification

Introduction

Methods for quantitative or semi-quantitative electrofishing have been previously evaluated for North American, European, Australian, and New Zealand fish assemblages (David et al. 2010; Kruse et al. 1998; Pusey et al. 1998; Sály et al. 2009). Published studies have produced mixed results, but generally support single-pass electrofishing as a robust proxy for total fish abundance in a stream reach. However, some New Zealand fishes are nocturnal, cryptic, reside in thick cover, or do not respond to electric current in a manner similar to salmonids and cyprinids (Graynoth et al. 2012). In particular, adult *Anguilla* spp. reside in undercut banks, tree roots, debris clusters, and heavily vegetated microhabitats, making them hard to detect and capture while electrofishing. Additionally, non-diadromous *Galaxias* spp. tend to flee and scatter from electric current rather than be drawn towards it as with salmonids and cyprinids. Most quantitative research employing electrofishing in New Zealand typically uses three passes with a stop-net set at the bottom of the reach to ensure that these elusive native fish are reliably captured (McIntosh 2000, McHugh et al. 2010). To evaluate the efficiency of my single-pass electrofishing methods, I compared different fish size and abundance metrics between single-pass and three-pass (stop-net) methods for 25 headwater streams in the Canterbury region of New Zealand (undertaken for a different research project from the one described in this manuscript).

Methods

I electrofished 50-m reaches with a downstream stop-net in February–March 2017. These reaches varied in size, discharge, hydrological disturbance regime, and riparian land cover. Captured fish were identified, measured, and recorded separately for each pass. Data from pass number one (minus the stop-net catch) were compared to data from all three passes plus the stop-net to calculate the efficiency of the single-pass method. Maximum fish size,

size range, mass–abundance slope, abundance, and biomass were compared between the single-pass and three-pass methods. This was tested by first working out the ratio for each metric (i.e., 1-pass value/3-pass value), then constructing a linear regression of the three-pass value (on *x*) versus this ratio (on *y*; what I termed as the 'ratio regression' in Table 2B.1; Kelly et al. 2005). The null hypothesis was that the relative efficiency (size of the ratio) would not be affected by absolute values (3-pass total) so the regression should be non-significant (p-val > 0.05). Habitat factors including dominant channel unit type (riffle, pool, or run), discharge, hydrological disturbance level, and stressors (agricultural influence, drying, abstraction, didymo presence) were included in models to assess if these affected single-pass electrofishing efficiency. I included the presence of Didymo (*Didymosphenia geminata*) as a possible stressor because it is an invasive diatom that has been linked to declines in trout abundance in New Zealand (Jellyman & Harding 2016). Additionally, I calculated species detection probability for the single-pass method.

Results/Discussion

Nine species of fish were captured, and 3505 individuals were identified and measured for this investigation. Single-pass species detection probability was affected by discharge and hydrological disturbance level, but was high overall (mean = 0.90). Species detection efficiency was most-often influenced by a single individual of a rare species being caught in the second or third pass, and thus lower detection probability had little effect on mass–abundance relationships or other body-size metrics.

Linear regressions relating three-pass and single-pass abundance, biomass, size range, and maximum size were highly significant ($R^2 > 0.90$; Table 2B.1), supporting a robust correlation between the two electrofishing methods for these metrics. Mass–abundance relationships between the two methods were slightly less-correlated ($R^2 = 0.66$; Table 2B.1). No habitat variables or their interactions significantly modulated the relationship between

single-pass and three-pass values. 'Ratio regression' tests for all metrics were not significant (p-val > 0.10; Figure 2B.1), showing that the relationships between the two electrofishing methods were not different, and that a simple correction could be made to relate single-pass metrics to three-pass electrofishing values.

Table 2B.1 Slope, y-intercept, R^2, and p-value of 'ratio regression' of single-pass vs. three-pass electrofishing methods for fish body size and abundance metrics in twenty-five Canterbury, New Zealand streams. See methods in Appendix 1 for description of the 'ratio regression.'

Metric	Slope	Y-intercept	R^2	Ratio regression (p)
Abundance	1.39	19.37	0.91	0.73
Biomass	1.33	116.66	0.94	0.38
Max body size	0.99	31.21	0.99	0.17
Size range	0.99	31.57	0.99	0.15
Mass–abundance slope	0.73	-0.35	0.66	0.81

These findings support the use of single-pass electrofishing as a valid and robust comparative method to the 3-pass quantitative method for measuring fish abundance and size structure. This is similar to the conclusions drawn by Kruse et al. (1998), Reid et al. (2009), Sály et al. (2009), and Graynoth et al. (2012) that have investigated the legitimacy of single-pass electrofishing, although Kennard et al. (2006) found that a slightly more-intensive single pass survey of multiple channel units yielded a more accurate estimate of stream fishes in Australia. However, the small sample size (n = 25 reaches) and limited geographic scope of this investigation (Canterbury region only) would lend to cautionary use of this method elsewhere. Researchers may want to conduct their own methods verification in a similar fashion if employing this method outside of Canterbury.

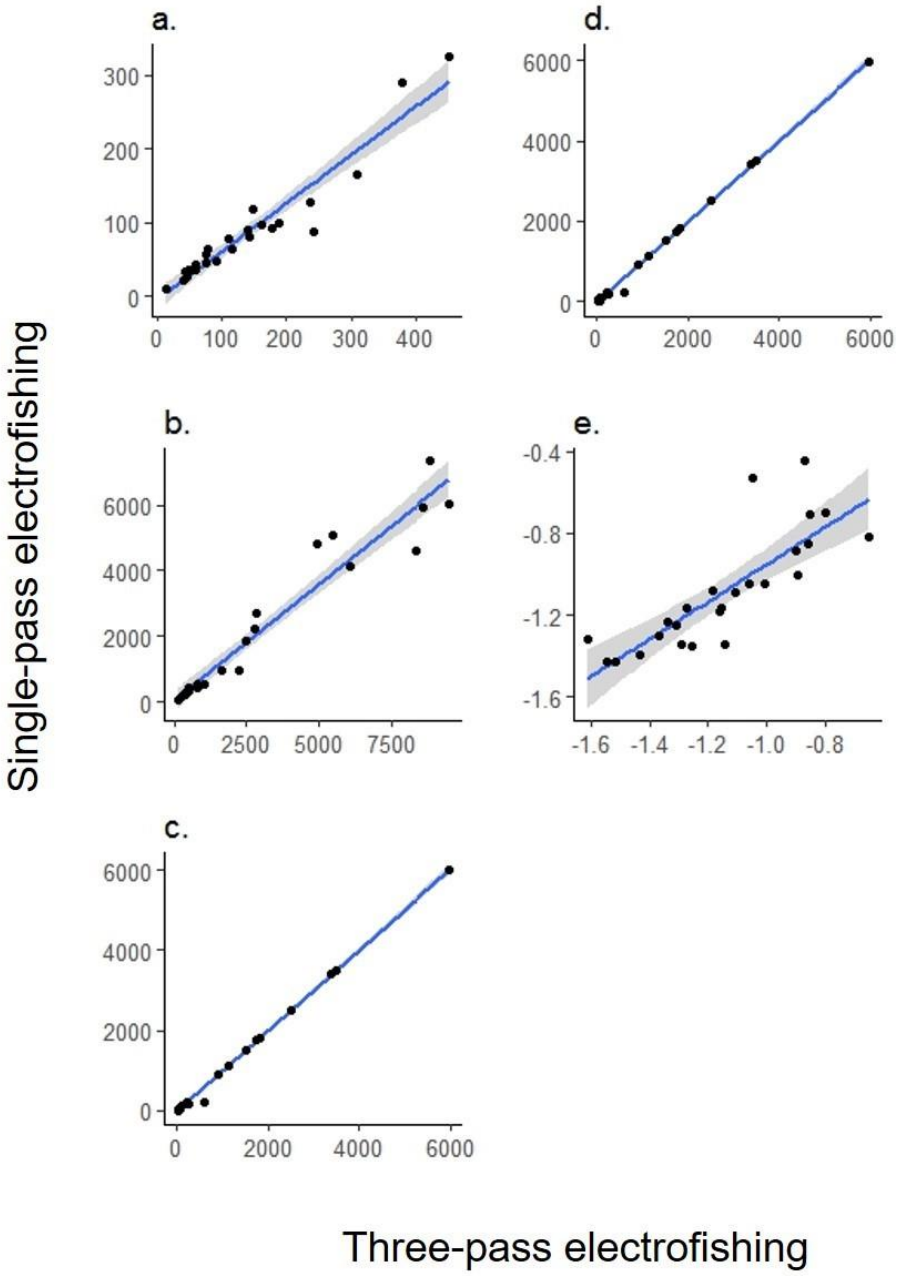

Figure 2B.1. Single-pass (y-axis) vs. three-pass (x-axis) electrofishing efficiency for fish abundance (a), biomass (b; grams/reach), maximum size (c; grams), size range (d; grams), and mass–abundance slope (e) for each of twenty-five fifty-meter Canterbury, New Zealand stream reaches. The lines illustrate ideal 1:1 ratio of maximum efficiency between the two methods. See Table 2B.1 for specific values.

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Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapter Three "Big impacts from small abstractions: the effects of surface water takes on freshwater fish assemblages" was coauthored by both Kevin Fraley and fellow PhD student Nixie Boddy, who equally contributed to the workload. This chapter also appears in Nixie's PhD thesis.

Please detail the nature and extent (%) of contribution by the candidate:

Supervisor Angus McIntosh assisted with study design and reviewed and provided suggestions for improvements on several drafts of the chapter. Other supervisors (Helen Warburton, Doug Booker, and Dave Kelly) reviewed at least one draft of the chapter and provided input on the data analysis approach. The workload was split evenly between Kevin Fraley and Nixie Boddy, as described in the following table.

Component	Nixie	Comments	Kevin	Comments
Abstraction site identification	50%	Tracked down 2/4 abstraction sites based on recommendations from NIWA, joint visits to possible sites	50%	Tracked down 2/4 abstraction sites using google earth, joint visits to possible sites
Study design (physical)	75%	Provided sampling scheme based on other work	25%	Input on sampling scheme, provided design for isotope sampling
Study design (conceptual)	60%	Joint development of hypotheses	40%	Joint development of hypotheses
Fieldwork	50%	Full participant in fieldwork at 60 stream reaches	50%	Full participant in fieldwork at 60 stream reaches
Labwork	0%	Was not involved with labwork	100%	Processing of 372 samples for nitrogen and carbon SI analysis
Data processing	60%	Derived "percent flow" habitat variable, calculated diversity measures, helped calculate abundance and biomass measures	40%	Calculated food-chain length, carbon range, mass–abundance, and native-introduced ratio responses, helped calculate abundance and biomass measures
Model design	50%	Constructed and modified Poisson distribution model sets	50%	Set up likelihood ratio tests and corrected for model overdispersion, assisted with model set construction
Data analysis, figures, tables	50%	Some stats work, generated figures	50%	Some stats work, generated tables
Writing: Structure, Intro, methods	50%	Contributed to introduction and methods sections. Extra lit search and organisation for intro.	50%	Wrote up initial manuscript outline, identified potential target journals, contributed to introduction and methods sections
Writing: Results and Discussion	50%	Figures, editing, native-introduced ratio idea	50%	Stats, data crunching, tables, initial pass on results and discussion organisation and text

Writing: Editing based on supervisor comments	50%	Abstract, introduction, results, discussion edits	50%	Abstract, methods, and discussion edits
Average contribution	***50%***		***50%***	

Certification by Co-authors:

The undersigned certifys that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

Name:	Signature:	Date:
Angus McIntosh		23/7/18

Chapter Three

Big impacts from small abstractions: the effects of surface water takes on freshwater fish assemblages*

A torrentfish captured downstream of a water abstraction on Taylors Stream during fieldwork for this Chapter.

*This Chapter was coauthored by fellow PhD student Nixie Boddy

Abstract

Abstractions and diversions are prevalent in river networks worldwide, however specific mechanisms and measures reflecting changes in functional characteristics of aquatic assemblages in response to flow abstraction have not been well established. In particular, despite being ubiquitous worldwide, the influence of small takes on fish assemblages is poorly understood. I used surveys and stable-isotope analyses to evaluate the impact of differing levels of flow abstraction on fish assemblage structure, and native-invasive patterns of coexistence, associated with small surface water abstractions in four streams in the Canterbury region of New Zealand. My study design accounted for longitudinal processes to isolate the effects of abstractions on fish assemblages. I found reaches with reduced flows downstream of abstraction points had significantly lower fish abundances per metre of stream length, likely due to decreased habitat size, altered interspecific interactions and barriers to movement. The loss of larger fish in reaches with high rates of flow removal resulted in shallower mass–abundance relationship slopes and shorter stable isotope-derived food-chain lengths, likely due to fewer trophic links in the food web. The large fish removed from these sites were flow-sensitive introduced salmonids, resulting in higher relative abundances of small-bodied native fish, likely due to predatory and competitive release. Small water abstractions can therefore alter both the structure and composition of stream fish assemblages, and modify the outcomes of native-invasive species interactions. Thus a better understanding of the effects of small abstractions could be used to improve the strategic management of fish in invaded riverscapes.

Introduction

Freshwaters across the globe are increasingly manipulated through dewatering, water diversion, and water abstraction as anthropogenic demands grow and the effects of climate change become more pronounced (Murchie et al. 2008). The modification of flow regimes is one of the most extensive anthropogenic alterations to lotic systems (Petts 1984; Stanford et al. 1996) and is often cited as the largest threat to freshwater ecosystems (Naiman et al. 1995; Sparks 1995; Lundqvist 1998; Ward et al. 1999). Some estimates suggest that over 50% of the largest river systems worldwide are moderately or severely impacted by flow regulation (Dynesius & Nilsson 1994; Nilsson et al. 2005). Thus, the potential ecological impacts of this widespread flow modification are of major concern, however little is known about the effects of small abstractions, particularly on fish assemblages, aquatic food chains, and influences on interactions between native and non-native taxa.

River abstractions and diversions tend to modify natural flow patterns and cause fluctuations in discharge (Murchie et al. 2008). Altering flows and abstracting water from rivers can often have negative impacts on flora and fauna, and can lead to species declines and local extinctions (Bunn & Arthington 2002; Dewson et al. 2007b; Benda et al. 2011). The effects of hydropower dams and large-scale diversions on aquatic communities have been well-documented (Poff & Zimmerman 2010), but the impact of small abstractions on watercourses is understudied, despite being much more common. For example, in New Zealand there are approximately 16,000 consented abstractions nationwide, with a mean water abstraction rate of 0.04 m^3/s, and 66% of these are for irrigation (Booker et al. 2016), so understanding the cumulative impacts of small irrigation takes is critical to the management of freshwater systems. Even small in-stream takes such as surface water abstractions and v-notch gauging weirs can impact flow regimes and hydraulic connectivity (Pusey et al. 1989; Bunn & Arthington 2002), and thus mobile organisms such as fish. It is

therefore important that the impacts of changes in flow regimes associated with small water abstractions on fish communities are well understood.

The relationship between flow regimes, habitat structure and fish communities has been well established (Poff & Allan 1995; Hart & Finelli 1999; Bunn & Arthington 2002), so it is unsurprising that modifications to natural flow regimes, such as water abstractions, will change physical habitat and influence fish population structure (Bunn & Arthington 2002). Most research on this subject has focused on abundance of target organisms (e.g., Leprieur et al. 2006), or occasionally species diversity, but effects at the whole community or assemblage scale have received less attention. Habitat contraction as a result of decreased river flow has been associated with changes in community composition and abundance (Stubbington et al. 2009; Datry et al. 2011), but understanding how trophic interactions respond to artificially decreased flows, could offer more insight into the processes driving these ecosystem shifts (McHugh et al. 2014).

The directional flow component of river systems means the effects of water abstraction should vary upstream and downstream of the abstraction point, however this has not previously been specifically considered. If fish passage is blocked, migratory species often decline or disappear from upstream reaches (Harris 1984; Bonetto et al. 1989; Joy & Death 2001). Reaches downstream of an abstraction will also be influenced by reduced flow, and can experience decreased fish abundance and maximum body size, and the loss of fluvial specialists in favour of generalist species (Haxton & Findlay 2008; Ledger et al. 2013; McHugh et al. 2014). Therefore, we should expect distinct changes in fish community composition and relative abundance upstream and downstream of abstraction intakes. Some of these directional shifts in community composition could arise from changes in flow regime modifying patterns of co-occurrence of native and non-native taxa.

While native fish are adapted to natural flow regimes, modifications to natural flows can facilitate the invasion of non-native species potentially better adapted to altered flow conditions. Moreover, because conditions in anthropogenically-altered systems tend to be similar regardless of geographical location (Bunn & Arthington 2002), this may result in homogenization of communities. Anthropogenic modifications often increase flow stability enabling introduced species to outcompete natives that are better adapted to high flow variability (Pusey et al. 1989; Bunn & Arthington 2002). I propose that for surface water takes, when a small proportion of the river is abstracted, flow could be moderated in favour of introduced species (Chen & Olden 2017), however when a large proportion of the river is abstracted, the resulting increased risk of extreme low flow and drought events creates much harsher environmental conditions that will benefit the species best adapted to low flow extremes. Therefore, the balance of native and non-native species relative abundance will depend on which group is more sensitive to extreme flows, and how the environment has shaped the evolution of native fish traits. For example, in situations where non-native trout are more sensitive to flow loss than native galaxiids (Leprieur et al. 2006) they were prevented from causing extirpations, thus flow abstraction can favour native fish species if they are better adapted to extreme flow conditions than non-natives (Chen & Olden 2017).

I examined the impact of small surface water abstractions, across a range of proportion of stream flow abstracted, on fish assemblages and derived metrics which reflected their functional and structural characteristics. These metrics included fish abundance, biomass, diversity, species richness, mass–abundance slope, maximum body size, carbon-range, food-chain length, and the ratio of native to non-native species abundance. Mass–abundance relationships derived from fish assemblage body-size relationships respond to habitat factors such as flood disturbance, flow, presence of predatory taxa, including non-native Salmonidae, and land cover (Layman et al. 2005; Chapter Two). Carbon range and

food-chain length, measures of the breadth and height of trophic relations respectively, can similarly be affected by many biotic and abiotic habitat factors (McHugh et al. 2014; Chapter Two).

I examined the effects of single-point surface water abstractions using a spatially-extensive longitudinal sampling approach. This included sampling an array of stream reaches above and below abstraction points to account for inherent longitudinal variability along the watercourses, and to enable me to isolate the direct effects of single-point water abstractions from other trends associated with local hydrology. I hypothesized that the proportion of flow abstracted, possibly interacting with direction to abstraction point (upstream or downstream) and/or distance to abstraction, would affect fish assemblage characteristics such as abundance and biomass (*H1*). This would potentially be due to effects of abstractions on directional connectivity, barriers to movement, and reductions in physical habitat size or productive space due to loss-of-flow. I expected that distance to abstraction location may be important due to a 'shadow' effect of the abstraction on biota, with groundwater recharge potentially mitigating flow loss further away from the abstraction point. I also predicted that the ratio of native to non-native species abundances would change, particularly downstream, with higher proportional native abundance in downstream sites with flows unsuitable for large-bodied non-native trout (*H2*). Finally, I posited that stable isotope-derived measures of trophic niche breadth, such as food-chain length and carbon range, would be similarly affected by flow abstracted, and direction and distance to abstraction (*H3*). Here I expected a loss of fish abundance and diversity would lead to fewer feeding options for biota, and thus a narrower prey range and decreased number of trophic links in reaches with high rates of flow abstraction.

Methods

Study site

One of the challenges of this type of study is the separation of direct effects of the modified flow regime from impacts associated with land-use change and intensification that are often associated with the development of such water resources (Bunn & Arthington 2002). New Zealand is an ideal study system because the headwaters of many foothill and mountain rivers remain relatively unimpacted by land conversion. Thus, I could target surface water abstraction sites on streams with unimpacted headwaters and large riparian buffers to minimise the confounding influences of land-use change and identify the direct effects of water abstractions on fish communities.

Four surface water diversions (termed 'sites') were surveyed in the Canterbury foothills, New Zealand. These abstractions were selected to incorporate a gradient of proportion of flow abstracted, and to include both dammed and undammed surface water diversions. All sites were subject to similar climatic conditions, distance to the ocean, and regional species pool (based on information from the New Zealand Freshwater Fish Database, McDowall & Richardson 1983), and all had relatively unimpacted catchments upstream of the abstraction point. To separate abstraction-related patterns from longitudinal stream trends, I structured my sampling reaches by splitting them into two sections: ten reaches upstream of the abstraction point, and five reaches downstream (Figure 3.1). A higher number of reaches were included upstream of the abstraction point to quantify natural flow variation and fish assemblage fluctuations for comparison with downstream abstraction-affected reaches. The length of each sampling reach was five times the stream width, and the distance between reaches was five times the average reach length for that section. Reach lengths were a constant multiple of mean stream width to avoid incorporating variability due to sampling different proportions of available habitat (Peterson & Ver Hoef 2010). Reach

lengths of five times the stream width were deemed sufficient to represent the habitat complexity in smaller streams, yet were not so large that reaches at larger streams were unachievable to sample in a day.

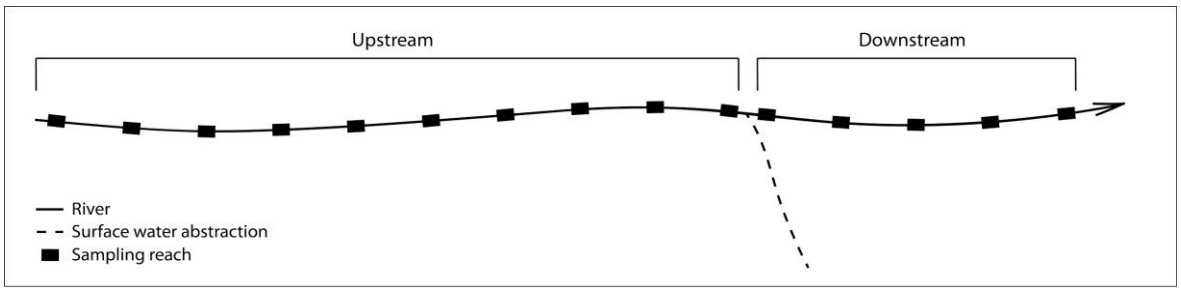

Figure 3.1. Schematic diagram of longitudinal sampling reaches around a surface water abstraction point. Ten reaches were sampled above the abstraction and five downstream. Each reach length was five times the average stream width, and distance between reaches was five times the reach length.

Habitat measurements

Seven ecologically significant habitat characteristics were measured for inclusion in analyses: Pfankuch River Disturbance Index (RDI), substrate size, stream width, depth, discharge, macrophyte cover and reach flow characteristics. Discharge was calculated at one transect per reach using the velocity-area method to create a cross-sectional discharge profile at each of five reaches evenly-spaced along the longitudinal gradient at each site (including directly above and below the abstraction point), and linear interpolation was used to derive flow for the reaches in-between. From discharge data, I calculated the proportion of maximum flow (%Flow) for each reach within each site as a proxy variable for effects of abstraction and any additional lateral or vertical flow exchanges between stream water and groundwater. Wetted width and water depth were measured along one transect at each reach. RDI, which is calculated by summing 15 aspects of channel morphology from the stream bed and banks to evaluate physical habitat stability and flood-proneness of a river channel (Pfankuch 1975; McHugh et al. 2010; Jellyman et al. 2013), was scored at every reach by the same person to ensure consistency. The percentage of the reach consisting of cascade, riffle,

run, and pool meso-habitat types (Maddock 1999) and the percentage area cover by in-stream macrophytes was estimated visually. The Wolman walk method was used to calculate mean substrate sizes from 50 randomly selected substrate particles measured along the beta axis (Green 2003). I also identified whether each stream reach was upstream or downstream of the abstraction point, and measured the distance from the abstraction point (Ups and DistA respectively; Table 3.1).

Fish capture and processing

Fish were caught using single-pass electrofishing conducted downstream into a push net using a Kainga EFM 300 backpack electrofishing machine (NIWA Instrument Systems, New Zealand) generating pulsed DC current. Single-pass electrofishing catch efficiency was verified through comparison with standard quantitative three-pass electrofishing using stop nets in a separate investigation to ensure that metrics generated were comparable (Appendix 2B). Fish were anaesthetized using AQUI-S^{TM} 20E (AQUI-S New Zealand Ltd.), counted, measured for total or fork length (species-dependent, mm), and each individual was identified to species. Six fish of representative taxa and sizes (spanning the smallest, medium, and largest) from each location were euthanized (if <400 mm TL) with an overdose of AQUI-S fish anaesthetic and frozen, or a non-lethal fin clip was taken (if >400 mm TL; Sanderson et al. 2009) and frozen for later stable isotope (SI) processing in the laboratory.

Table 3.1. Predictor and response variables evaluated in quasi-Poisson generalized linear models. Responses were converted to count data (multiplied by 1000) for purposes of rescaling and to fit my Poisson modelling framework, except for mass–abundance slope (kept untransformed for use in a linear model). See methods for detailed description of datasets and variables.

Type	Variable	Abbreviation	Units	Reference
Response	Abundance per metre reach length	Abundance	Fish/m	N/A
	Median body mass	Median	g	N/A
	Biomass per metre reach length	Biomass	g/m	N/A
	Shannon diversity index	Shannon	Unitless	Weaver & Shannon (1949)
	Ratio of native fish abundance to trout abundance	Native-trout ratio	Unitless	N/A
	Mass–abundance relationship slope	Mass–abundance slope	Unitless	Jennings et al. (2002)
	Mass–abundance relationship slope (extreme %Flow values only)	Mass–abundance slope (extremes only)	Unitless	N/A
	Food-chain length ($\Delta\ \delta^{15}N$)	FCL	Unitless	Post et al. (2000)
	Carbon range ($\Delta\ \delta^{13}C$)	CRange	Unitless	McHugh et al. (2014)
Predictor	Proportion of maximum stream flow (stream-specific)	%Flow	%	N/A
	Upstream or downstream from abtraction point	Ups	2-level factor	N/A
	Distance from abstraction point	DistA	Metres	N/A
	Abstraction site identity	StreamID	4-level factor	N/A

Fish assemblage and native-introduced metrics

Fish mass (g) was calculated from field-measured total or fork length (depending on species morphology), using regressions relating fork length, total length, and mass of New Zealand fish species (Jellyman et al. 2013). A subset of fish euthanized for this study were measured in the field and weighed in the laboratory to verify the applicability of these published relationships ($R^2 > 0.95$ for all species). Additionally, to construct mass–abundance relationships (also known as size spectra), individual fish mass was log-transformed and

binned in even steps along a $\log_{10}$ scale to best fit the range of fish body sizes at my reaches, and abundance of fish in each bin was also $\log_{10}$-transformed. A linear regression was constructed relating $\log_{10}$ binned abundance to the midpoints of $\log_{10}$ binned fish mass, and the slope was extracted to use as a response variable (mass–abundance relationship slope, Table 3.1; Jennings et al. 2002; Chapter Two). Other responses were calculated for fish assemblages in each reach, including: Shannon-Weaver diversity index (Weaver & Shannon 1949), median fish body mass (B50; g), total biomass (g/m), and abundance (no. fish/m, Table 3.1). Additionally, I calculated simple abundance and biomass ratios between native fishes and introduced brown trout (*Salmo trutta*), the only non-native species present, to see if abstractions differentially affected native and non-native fishes. Responses were converted to count data (multiplied by 1000) for purposes of rescaling and to fit my Poisson modelling framework, except for mass–abundance slope and native-introduced ratios (kept untransformed for use in linear models).

Stable isotope preparation and analysis

Primary consumers (*Deleatidium* spp. mayflies) were collected using a kick-net at each of the five reaches sampled for discharge (netted from three or more locations within each reach), and frozen for transport back to the laboratory. *Deleatidium* were chosen as a baseline consumer because they are ubiquitous in New Zealand, were present at all abstraction sites, and are commonly utilized by fishes as prey (Chapter Two). Primary consumers were utilized as a baseline to compare with fish for SI food-chain length analysis (McHugh et al. 2012). In the laboratory, *Deleatidium* from each reach were dissected and the stomach contents and head removed to eliminate potential bias from SI values (Lancaster & Waldron 2001). Composite *Deleatidium* samples were gathered from n = 20–100 individuals from each reach, following methods for composite samples from Post (2002). Fish were dissected and a portion of dorsal muscle tissue was extracted, or fin tissue was substituted for

individuals >400 mm to avoid lethal sampling (Hanisch et al. 2010). Next, fish and invertebrate tissues were dried in an oven for at least 72 hours at 50 °C, then ground into a fine powder using a mortar and pestle, with care taken to avoid contamination. Approximately 2 mg of powder from each sample was placed in an 8 × 5 mm tin capsule, folded, and sent to the University of California-Davis Stable Isotope Facility for analysis through isotope ratio mass spectrometry (on a PDZ Europa 20-20; Sercon Ltd.).

The resulting nitrogen isotope ratios were used to calculate trophic position (TP) of the sample organism, using an equation from Post (2002), as applied to similar streams by McHugh et al. (2012). The highest fish TP value from each reach was used as an estimate of food-chain length for the reach. Carbon isotope values were corrected for lipid content using established relationships (Post et al. 2007). Carbon isotope ratio range was calculated for fishes from each reach following the equation from McHugh et al. (2014). For brown trout it was not necessary to correct fin clip SI values to muscle values per McCarthy and Waldron (2000), who found no significant differences between tissue types for this species, but corrections were needed for fin clips from the only other species >400 mm found in my study area, longfin eel (*Anguilla dieffenbachii*).

Data analysis

I evaluated the relationship between responses (*H1*: fish abundance, mass–abundance slope, biomass; *H2*: native-introduced abundance ratio; and *H3:* FCL, and CRange) and predictor variables (%Flow, Ups, DistA) using reaches within abstraction sites as replicates (Table 3A.1). A term, including a variable identifying the stream sampled (StreamID), was included in each model (StreamID * Ups + DistA; Table 3.1) to account for my nested study design and structure the degrees of freedom to reduce the possibility of Type I errors (Dormann et al. 2007). Non-collinearity of predictors was verified by calculating variance inflation factors (VIF; cutoff ≥ 5), and some predictors originally tested (including RDI,

Wolman walk substrate size, macrophyte cover, stream depth, and wetted width) were eventually removed from models to eliminate overfitting or because they did not contribute to explaining variance in the data. The distance from abstraction variable (DistA) was scaled (centred and transformed to have a similar range to other variables) to eliminate model convergence errors. A saturated quasi-Poisson generalized linear model was constructed for most response variables (except for mass–abundance and native-introduced abundance ratio) using the (glm) function in R version 3.4 (R Development Core Team 2016). Quasi-Poisson models, fitted using the 'quasipoisson' link in the 'glm' function, were used to deal with the overdispersion present in standard Poisson models (Zeileis et al. 2008). Simple linear models using the 'lm' function were constructed for mass–abundance slope and native-introduced abundance ratio responses. Models with various interactions between predictors were compared to evaluate the importance of proportion of flow remaining (%Flow), distance from abstraction (DistA), and direction to abstraction (upstream or downstream; Ups) on fish assemblages, and to test all hypotheses. Using analysis of deviance for 'glm' models and analysis of variance for 'lm' models (ANOVA), predictors within the global model for each response were evaluated for significance ($\alpha < 0.05$).

Pseudo R^2 (McFadden's R^2; Faraway 2016) was also calculated for each response to assess goodness-of-fit of the saturated model compared to that achieved by a null model including a single parameter representing the intercept term. For analysis of the mass–abundance slope predictor, I also constructed a model assessing only reaches with the lowest and highest %Flow values upstream and downstream of the abstraction point at each site to minimize noise in the data occurring when all reaches were included in the original mass–abundance model. Four downstream reaches at the Kowai River site had 100% flow loss and no fish present, and these were omitted from my analyses. The entire Kowai site was also removed for the mass–abundance slope analysis because there was only one downstream

reach that had water and I required both minimum and maximum flow reaches for my analysis. Partial effects plots of the model results were produced using the 'ggplot2' (Wickham 2009) and 'effects' (Fox 2003) packages.

Results

Site and habitat characteristics

Some predictors originally tested (including RDI, Wolman walk substrate size, macrophyte cover, stream depth, and wetted width) were removed from models to eliminate overfitting or because they did not contribute to explaining variance in fish assemblages. Of the four abstraction sites sampled, a marked decrease in flow occurred downstream of the abstraction point in three sites, but flow temporarily increased in Taylors Stream due to a drain input just upstream of the abstraction (Figure 3A.1). Average discharge at the time of sampling ranged from <0.01 m^3/s in the smallest waterway (Limestone Creek) to 0.87 m^3/s in the largest waterway (Taylors Stream; Table 3A.1), and percentage of total flow loss from a combination of abstraction and downwelling varied between 57% in Taylors Stream to 100% in the Kowai River (where four of the reaches downstream of the diversion were dry). River Disturbance Index, averaged per site, ranged from 65 (low flood disturbance) in Limestone Creek to 116 (high flood disturbance) in the Kowai River, thus my sites encompassed a range of natural flood disturbance regimes.

Fish assemblages

The 4,457 fish caught included native Canterbury galaxias (*Galaxias vulgaris*), upland bully (*Gobiomorphus breviceps*), longfin eel, torrentfish (*Cheimarrichthys fosteri*), and introduced brown trout, with species richness varying among reaches from one to five taxa (Table 3A.1). The most ubiquitous species across sites were *G. breviceps* and *G. vulgaris* (present at all four sites), while *C. fosteri* were least widespread (only one site). Across sites, the most abundant taxa were *G. breviceps* (72.1% of total catch) and *G. vulgaris*

(21.2%), and the most uncommon were *A. dieffenbachii* (0.1%) and *C. fosteri* (0.2%). Total fish biomass across sites was dominated by *S. trutta* (42.8%) and *G. breviceps* (25.9%), with *C. fosteri* (< 0.1%) and *G. vulgaris* (13.1%) contributing the least. Given the rarity of native predatory fish (longfin eels) in these systems, non-native trout were an important predator in these fish assemblages.

Quasi-Poisson models predicting fish assemblage metrics performed substantially better than the null models in most cases (pseudo-$R^2 > 0.5$; Table 3.2), with the exception of fish biomass (pseudo-$R^2 = 0.17$). The linear model (not quasi-Poisson) predicting mass–abundance slope had poor explanatory power (adjusted $R^2 = 0.08$), however the mass–abundance model including only reaches with the lowest and highest %Flow upstream and downstream of the abstraction points performed much better (adjusted $R^2 = 0.65$).

Table 3.2. Characteristics of saturated quasi-Poisson generalized linear models for fish assemblage responses. The nested study design was accounted for with a StreamID*Ups + DistA term in all models (not presented here; see text for explanation). See Table 3.1 and Methods for explanation, coding, and units of variables. Pseudo R^2 refers to McFadden's pseudo R^2, which is a comparison of goodness-of-fit between the saturated model (as presented in this table) and a null model with only an intercept term.

Response	Structure	Degrees of freedom (null)	Residual deviance (null)	Pseudo R^2
Abundance	Ups * %Flow	45 (55)	27 (154)	0.82
Biomass	Ups + %Flow	46 (55)	620 (738)	0.16
Shannon	Ups + %Flow	46 (55)	3561 (7434)	0.52
Native-trout ratio*	Ups * %Flow	23	7.43	0.60
Mass–abundance slope*	Ups + %Flow	46	0.32	0.04
Mass–abundance slope*	Ups * %Flow	3	0.21	0.65
FCL	Ups * %Flow	45 (55)	682 (1094)	0.38
CRange	Ups + %Flow	46 (55)	26049 (37129)	0.30

*The models for mass–abundance slope and native-trout ratio are simple linear models (not quasi-Poisson glm like the others) and the residual standard error and adjusted R^2 are shown in place of residual deviance and pseudo R^2, respectively.

ANOVA indicated that %Flow and Ups factors interacted to significantly affect fish abundance and the mass–abundance relationships (for lowest and highest flow reaches) at my abstraction sites (Table 3.3, Figures 3.2 and 3.3). This indicated that the number of individuals per metre of stream length, and the size structure and abundance within the assemblage, were significantly influenced both by the amount of water abstracted and the direction from the abstraction point (supporting *H1*).

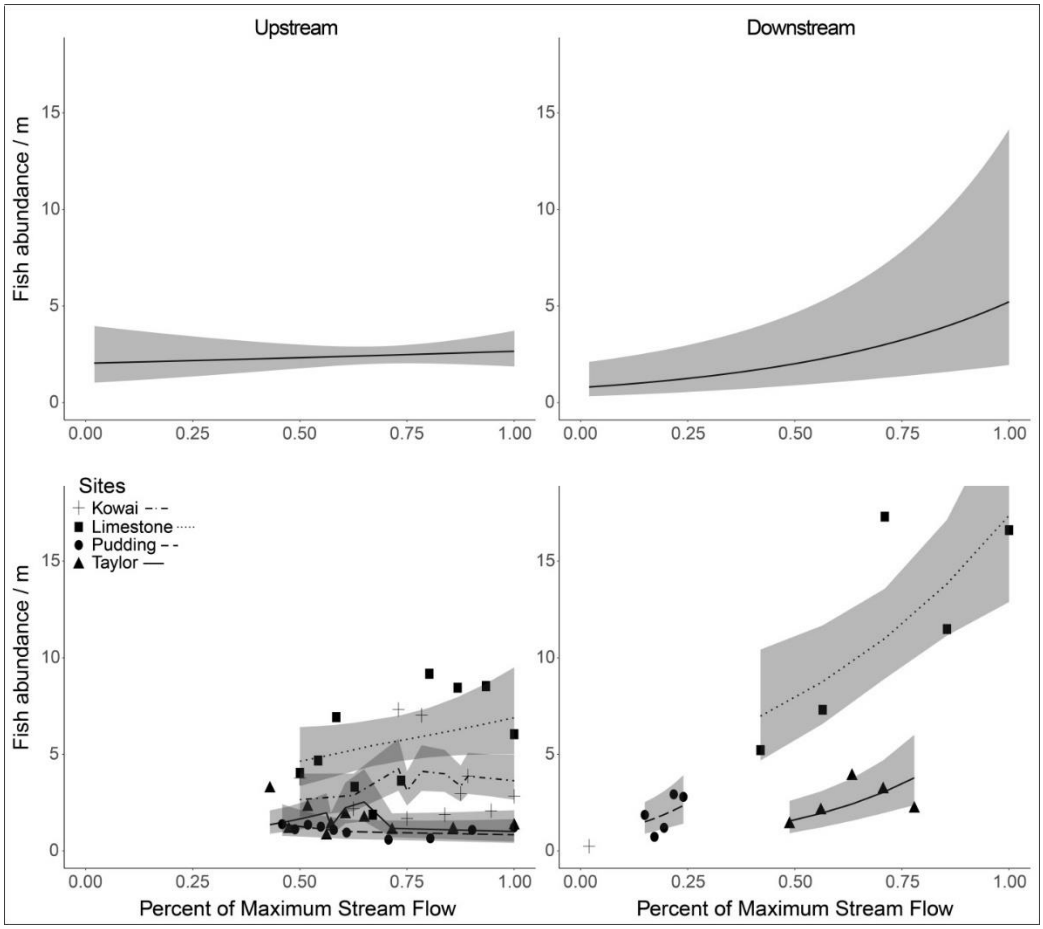

Figure 3.2. Total fish abundance per m of stream length, depending on proportion of maximum stream flow and direction to abstraction (upstream or downstream). Top panel shows partial effects plots and bottom panel shows predicted values for each observed data point. Note predicted lines in the bottom panel will not necessarily be smooth because each prediction is influenced by the observed points' distance to confluence. Lines represent model estimates with 95% confidence intervals displayed as grey bands. Points show raw data with shapes representing the site each sample was taken from. See Table 3.1 for explanation of variable derivation and units, and Table 3.3 for statistical values.

Upstream of the abstraction point, fish abundance did not vary with decreasing proportion of maximum flow (Figure 3.2). Downstream however, abundance declined with decreasing %Flow, and downstream reaches with high %Flow contained higher fish abundances than reaches with equivalent flows upstream (Figure 3.2, Table 3.3). Natural flow fluctuations modified flow upstream of abstractions by up to 50%, however no significant change in fish abundance per metre of stream length was seen associated with this natural flow variability. Similarly, with mass–abundance slope (for highest and lowest %Flow upstream and downstream at each site), there was minimal change in the relationship upstream of the abstraction; a slightly increasing mass–abundance slope did indicate a shallower (but negative) distribution of fish size class abundance (Figure 3.3).

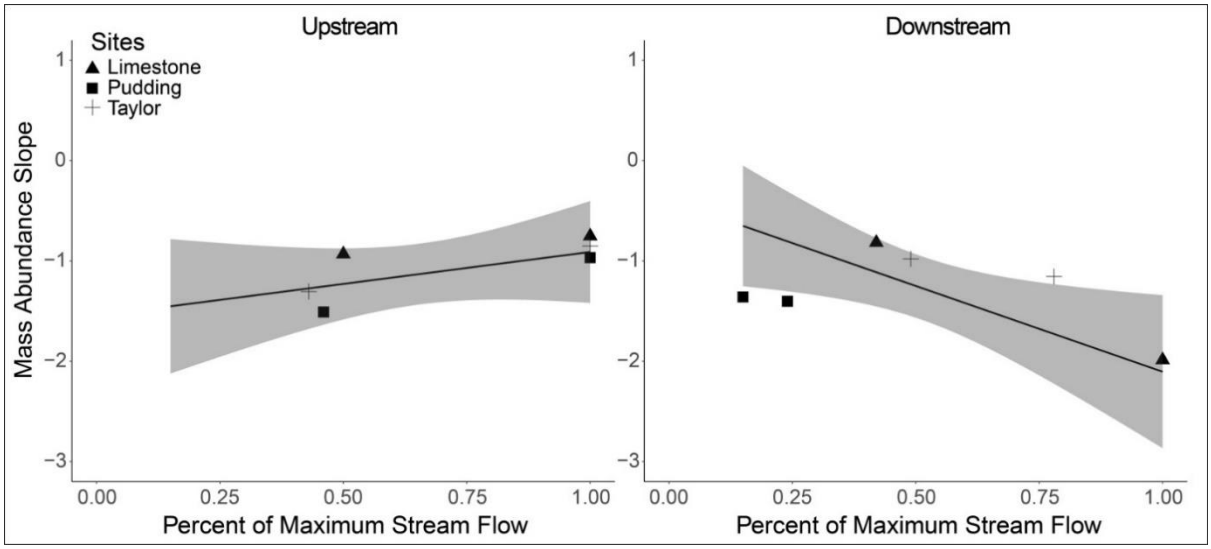

Figure 3.3. Partial effects plots showing significant interactions between proportion of maximum stream flow and direction to abstraction (upstream or downstream) on mass–abundance slope for a subset of stream reaches at each site. Lines represent model estimates with 95% confidence intervals displayed as grey bands. Points show raw data with shapes representing sites. The subset is limited to the reaches which have the lowest and highest %Flow values upstream and downstream at each site. The Kowai River site is not included because only one reach downstream of the abstraction contained fish. See Table 3.1 for explanation of variable derivation and units, and Table 3.3 for statistical values.

However, downstream of the abstraction, the slope became more steeply negative. The driver of this interaction was the loss of larger body size-classes of fish with decreased flow in downstream reaches (See Figure 3A.2 for visualization of this). There was no evidence of an additional significant interaction between %Flow, Ups, and for any of the response variables, nor was DistA a significant main effect.

Native-introduced fish relative abundance

Fish assemblages were numerically dominated by native fish (from 6 to 33 times more abundant) and for the three abstraction sites sampled where non-native brown trout were present, they comprised between 1.3 to 5 times more biomass (Limestone Creek did not contain any trout; Table 3A.1). At the two sites where trout were present and with suitable replication of reaches both upstream and downstream of abstraction (Taylors Stream and Pudding Hill Stream), native fish abundance increased relative to trout with decreased %Flow both upstream and downstream of abstraction points (Table 3.3, Figure 3.4). The relationship, however, was much stronger in downstream reaches, with rapid decreases in co-occurrence as local flow declined. Interestingly, at the downstream reaches at both sites, the largest fish in reaches with highest %Flow were brown trout, while the largest fish in reaches with lowest %Flow were native taxa. My linear model predicting the relative abundance of native and introduced fish explained variance in the data well (adjusted $R^2 = 0.60$; Table 3.2), underscoring the explanatory power of flow and habitat size in determining the outcome of interactions between native and introduced taxa.

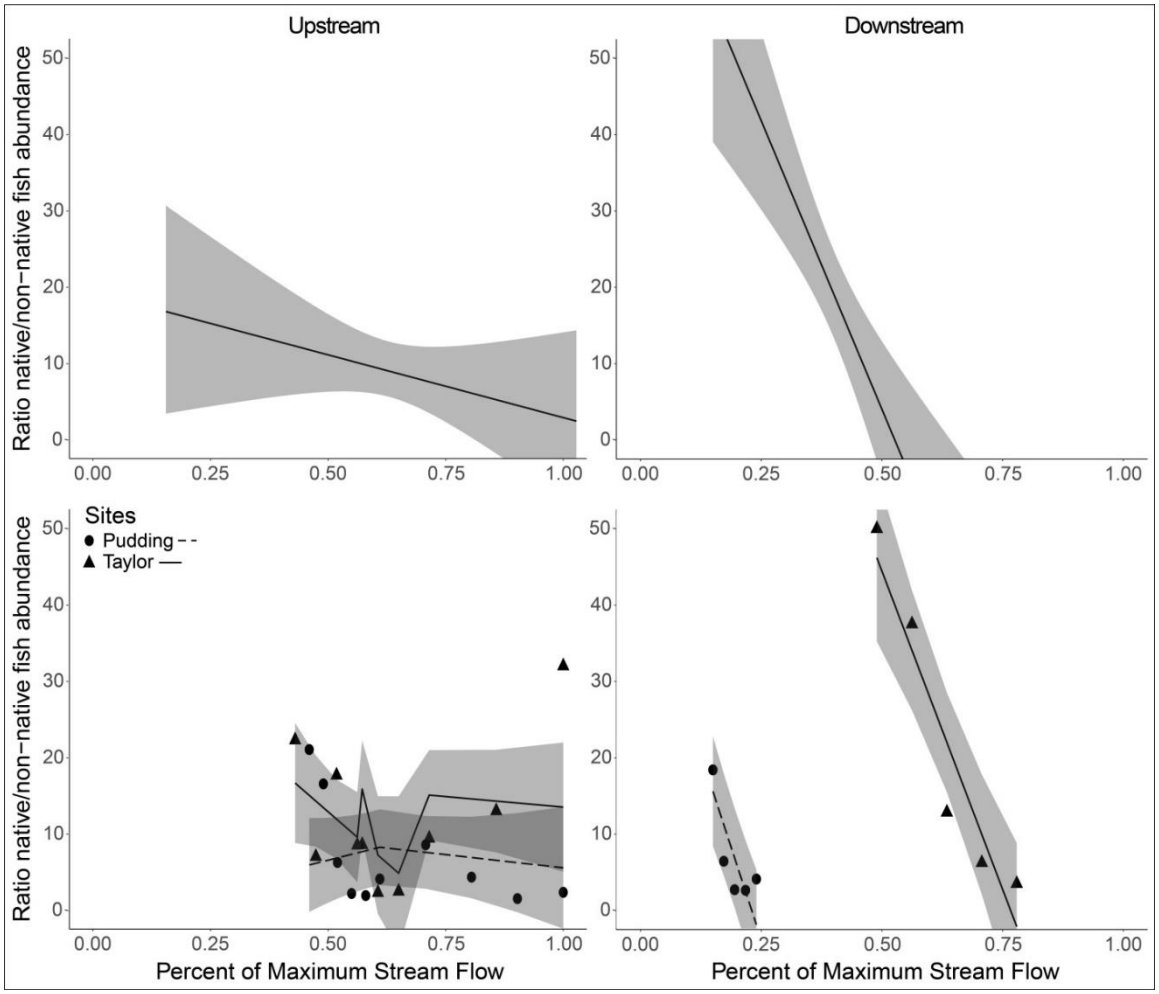

Figure 3.4. Proportion of the fish assemblage that was native compared to non-native, depending on a significant interaction between proportion of maximum stream flow and direction to abstraction (upstream or downstream). Top panel shows partial effects plots and bottom panel shows predicted values for each observed data point. Note predicted lines in the bottom panel will not necessarily be smooth because each prediction is influenced by the observed points' distance to confluence. Lines represent model estimates with 95% confidence intervals displayed as grey bands. Points show raw data with shapes representing sites. The Limestone River site was not included because no non-native fish were captured at any reach, and the Kowai River site was not included because the reach downstream of the abstraction did not contain non-native fish. See Table 3.1 for explanation of variable derivation and units, and Table 3.3 for statistical values.

Food-chain length and carbon range

Relative to fish assemblage metrics, quasi-Poisson models relating stable isotope-derived metrics to proportion of flow abstracted did not explain as much variance (pseudo-R^2 < 0.4; Table 3.2). No significant relationships were found with carbon range predictors, indicating little change in trophic breadth (Table 3.3). However there was a significant interaction between %Flow and position upstream or downstream of the abstraction affecting

food-chain lengths, with decreases in FCL downstream of abstractions. Thus, abstractions did influence stable isotope-derived metrics downstream, by reducing the number of trophic links in the fish assemblage when higher proportions of the flow were removed (supporting *H2*).

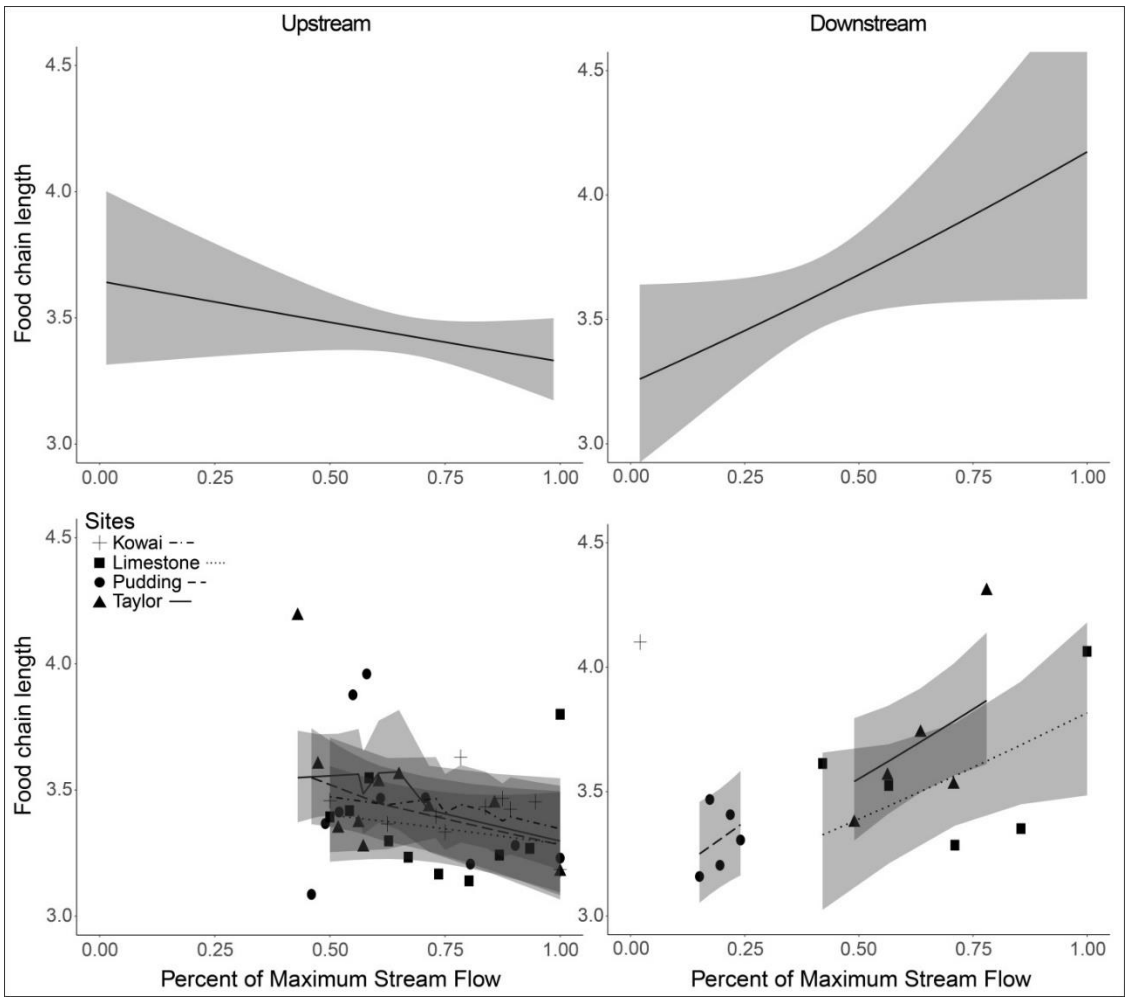

Figure 3.5. Food-chain length, depending on proportion of maximum stream flow and direction to abstraction (upstream or downstream) on food-chain length. Top panel shows partial effects plots and bottom panel shows predicted values for each observed data point. Note predicted lines in the bottom panel will not necessarily be smooth because each prediction is influenced by the observed points' distance to confluence. Lines represent model estimates with 95% confidence intervals displayed as grey bands. Points show raw data with shapes representing the site each sample was taken from. See Table 3.1 for explanation of variable derivation and units, and Table 3.3 for statistical values.

Food-chain length increased with decreasing proportion of flow upstream of abstractions (supporting *H3*). The effect was inverted downstream, and trophic changes were much steeper, indicating food chains rapidly decreased in length as local flow decreased

(Figure 3.5). This was driven primarily by a loss of larger-bodied fish (Figure 3A.2), typically brown trout at the top of the food chain, in downstream reaches with lower local flow. Overall food-chain lengths in these systems were highly variable, as the weak model fit suggests. There was no evidence of an additional significant interaction between %Flow and Ups for any of the response variables, nor was DistA a significant main effect.

Table 3.3. Analysis of deviance and variance and summary output for quasi-Poisson generalized linear models ('glm') and simple linear models ('lm') for fish assemblage responses. Model structure is specified in Table 3.2. Responses were converted to count data (multiplied by 1000) to fit my Poisson modelling framework, except for mass–abundance slope, which used a linear model. See Table 3.1 and methods for explanation, variable definitions, and units of variables.

Response	Predictor	Estimate (Std. error)	F-value	P-value
Abundance	Ups*%Flow	-1.64 (0.70)	5.57	0.02
	%Flow	1.90 (0.51)	17.69	<0.01
	Ups	3.18 (2.06)	19.81	<0.01
	DistA	-0.24 (0.10)	1.12	0.30
Biomass	%Flow	-0.03 (1.06)	0.77	0.38
	Ups	4.31 (8.58)	0.07	0.79
	DistA	-0.16 (0.20)	0.94	0.34
Shannon	%Flow	0.33 (0.32)	0.48	0.49
	Ups	0.14 (0.42)	0.13	0.72
	DistA	-0.01 (0.06)	0.03	0.86
*Native-trout ratio**	Ups*%Flow	-134.34 (38.55)	12.14	<0.01
	%Flow	-16.89 (13.76)	72.92	0.26
	Ups	20.68 (12.05)	2.80	0.11
	DistA	3.96 (2.42)	4.10	0.05
*Mass–abundance slope**	%Flow	-0.15 (0.29)	0.98	0.33
	Ups	0.04 (0.20)	2.61	0.11
	DistA	0.03 (0.06)	0.01	0.93
*Mass–abundance slope (extremes only)**	Ups*%Flow	-2.35 (0.58)	3.20	0.03
	%Flow	0.64 (0.37)	0.52	0.52
	Ups	1.19 (0.47)	3.20	0.17
	DistA	0.03 (0.12)	0.08	0.79
FCL	Ups*%Flow	0.34 (0.14)	5.64	0.02
	%Flow	-0.09 (0.07)	<0.01	0.95
	Ups	0.10 (0.08)	4.59	0.04
	DistA	-0.01 (0.01)	2.01	0.16
CRange	%Flow	0.19 (0.38)	0.05	0.82
	Ups	1.12 (0.41)	2.90	0.10
	DistA	-0.01 (0.01)	0.23	0.63

*The models for mass–abundance slope and native-trout ratio are simple linear models (not quasi-Poisson glm like the others).

Discussion

Recognition that anthropogenic alteration of flow regimes is a threat to aquatic ecosystems globally has led to increasing interest in understanding the responses of aquatic ecosystems to different types and degrees of flow alteration (Dudgeon et al. 2006; Poff & Zimmerman 2010). Only a handful of studies in temperate-region rivers have examined the effects of small abstractions, with widely varying conclusions. Several of these projects found little or no detrimental impact of abstraction on the study organisms (Leprieur et al. 2006; Dewson et al. 2007a; Lange et al. 2014), while others found negative effects on the abundance and diversity of organisms downstream of abstraction (Death et al. 2009; Matthaei et al. 2010; Falke et al. 2011). My investigation showed that flow loss downstream of surface water abstractions significantly affected fish abundance, mass–abundance slope, food-chain length, and relative abundance of native and introduced fishes. As I expected, these effects depended on spatial position relative to the abstraction point, with downstream reaches affected to a greater degree than upstream areas. However, there was no additional interaction with distance from the abstraction point as I hypothesized. Given the high proportion of rivers globally that are potentially impacted by small abstractions (Anderson et al. 2006; Deitch et al. 2009), the effects they can have on fish assemblages, such as those outlined below, are likely to be extremely influential.

Effects of water abstraction on fish assemblages

Abstractions likely affected fish assemblages through reduced quantity and quality of physical habitat associated with decreased wetted width, depth and water velocity, possibly by prevention or interruption of fish movement upstream or downstream of diversion points. As predicted in *H1*, fish abundance was lower below abstraction points when flow loss was high, and mass–abundance relationships (at extreme %Flow values at each reach) had steeper slopes. In terms of abundance, the loss-of-flow downstream of abstraction points typically

resulted in smaller habitat sizes, potentially reducing carrying capacity for fishes, but no statistically significant decreases in biomass or fish diversity were detected. For mass–abundance slope, reaches with the highest %Flow downstream of abstractions had higher abundance of small-bodied fish but larger-bodied size classes were absent. This may be caused by large-bodied fish, such as trout, leaving abstraction-exacerbated low flow reaches, while small-bodied native fishes such as galaxiids and bullies either remained because they were less affected (similar to findings of Leprieur et al. 2006), or possibly were released from predation by trout. In contrast, similar research from tropical Central America found that fish assemblage composition, but not abundance, changed upstream and downstream of abstraction sites on small, mountainous streams (Anderson et al. 2006).

Using my longitudinal sampling design, I was interested in how fish assemblage structure changed in relation to natural flow variation, due to upwelling and downwelling, compared to artificial changes in flow associated with abstractions. Surface water-groundwater interactions such as these are common in many rivers globally that have large gravel floodplains (Brunke & Gonser 1997). The significance of the interaction between proportion of flow loss and direction (upstream or downstream) from the abstraction point indicates that the assemblage composition and the relative abundance of different size-classes of fish were only affected by loss-of-flow caused by the artificial abstraction, and not by natural fluctuations in flow caused by groundwater losses or gains. Flow loss caused by abstraction can be clearly visualized and compared with variability resulting from groundwater losses or gains in Figure 3A.1. These results suggest there is a fundamental difference in fish assemblages' ability to cope with and respond to natural versus anthropogenic flow variation.

One of my abstraction sites (Limestone Creek) had a partial fish movement barrier associated with the abstraction, and all sites had diversion channels without fish exclusion

devices, in which fishes could become entrained, which may explain some of the interacting effects of flow loss and flow direction from the abstraction point. While these diversion channels were not flowing at high velocity, it would be easy for downstream-migrating fishes to choose to swim into them, which could result in disorientation or mortality due to desiccation or water intake machinery (e.g., pumps), depending on the terminus of these channels. This may be a particularly important mechanism when a high proportion of river flow is being extracted, which may be associated with the low abundances I found at low proportion-flow sites. A similar project looking at abstractions in Puerto Rico, USA, found that freshwater shrimps similarly increased in abundance downstream of a small dam that was a partial migration barrier, and that up to 100% of downstream-migrating shrimp larvae were entrained into the intake of the associated abstraction (Benstead et al. 1999). While I did not monitor entrainment of fishes into the surface-water intakes, this would be a useful future avenue of research to explain the mechanisms behind upstream-downstream differences in fish communities.

Effects on native and introduced species

Similar to predictions in *H2*, there were higher numbers of native fishes at reaches with greater flow loss from abstraction, relative to numbers of introduced brown trout. Unlike trout, New Zealand native fishes are adapted to living in smaller, often benthic habitats, and in the case of galaxiids, even occupying streambed interstitial spaces (Davey et al. 2006). For example, the reaches I sampled downstream of the abstraction on the Limestone Creek consisted of very shallow water flowing through rock matrices, yet they were populated by hundreds of upland bullies. Thus, native fish could have higher relative abundances downstream of abstractions either due to the absence of trout (less predation and competition) or due to a preference for the habitat characteristics caused by the abstractions. However, this does not necessarily mean native fish were thriving in these areas of flow loss, because they

may have also been negatively impacted, just to a lesser degree than trout. In this instance, areas of refugia from trout predation may not be optimal habitats for native fishes, just preferable to the alternatives.

Despite the possibility of easy trout access to the reaches downstream of the abstraction intake on Limestone Creek via a connection to the Hinds River (a higher-order river downstream), trout were completely absent in all reaches. This is likely due to trout preference for deeper pools (for refuge; Davey & Kelly 2007) and need for habitats with enough flow to deliver drifting invertebrate or terrestrial prey (Hughes et al. 2003). Additionally, trout are known to be averse to human activity and movements on the streambank (Young & Hayes 2004), perhaps causing them to avoid areas adjacent and downstream of abstraction intakes, which have higher likelihood of human visitation (i.e., abstraction structure maintenance activity and paths allowing easy access for fishermen or hikers). In areas with more flow, trout abundance relative to native fishes increased, although native fishes were still more abundant overall at all reaches (but did not always dominate in terms of biomass). This is likely due to the propensity of trout to prey upon or out-compete native fishes, especially galaxiids, when occurring in sympatry (McIntosh et al. 2010).

There is a scarcity of research on the effects of small-scale abstractions and diversions on patterns of native and introduced fish co-occurrence globally, particularly for temperate fresh waters, so my findings could be particularly useful to aquatic ecosystem managers. Other studies in New Zealand also concluded that trout presence was negatively correlated with percent of water abstracted, however corresponding effects on native upland bullies or roundhead galaxias (*Galaxias anomalus*) were quite different in that native taxa showed no response (Leprieur et al. 2006; Lange et al. 2014). This supports my contention that loss-of-flow from abstractions may be detrimental to large-bodied fishes (i.e., trout) and offer some relief to native taxa (i.e., bullies and galaxiids) by offsetting effects of non-natives. Many

studies report native fishes suffer in relation to introduced taxa because flow modifications cause more benign habitats for invaders and poorly fit the ecological adaptations of native fish (Merciai et al. 2018), but in the case of my study, the non-native species was more sensitive to anthropogenic habitat alterations than native fishes, leading to a contrasting result. There are other rare instances, similar to my findings, where flow modifications have been found to favour native taxa (e.g., dam blocking spread of introduced trout; Lintermans 2000). The increase in relative abundance of native fish downstream of surface-water abstractions, associated with higher flow loss, could be attributed to the flexible life-history patterns of New Zealand fish species that have developed as a response to highly variable and unpredictable flow regimes (Winterbourn et al. 1981; Lake et al. 1985), enabling these taxa to cope with unpredictable flow changes associated with human demand around water abstraction sites, unlike non-native trout species (Jowett & Biggs 2009). While native fish were able to persist in these highly-impacted locations, there is no evidence for how negatively-affected the long-term health and viability of these populations are by the flow loss, for example through reduced survival or recruitment, and increased vulnerability to natural flow extremes compounding anthropogenic drying effects.

Effects on food-web characteristics

Following my expectations from *H3*, abstractions affected food-chain lengths downstream of abstraction points, although there was no associated modulation of carbon range of fish diets, which suggests there was no change in trophic breadth, but trophic height was reduced. The decrease in food-chain length with loss-of-flow below abstractions may be partially explained by the disappearance of larger-bodied fishes, which typically have higher trophic positions (Arim et al. 2010; Chapter Four; thus reducing the number of trophic links in the food web). A positive association between habitat size and food-chain length has been documented across a wide range of ecosystems (Sabo et al. 2010), and alterations in trophic

height have often been driven by changes in the abundance or presence of large top predators (McHugh et al. 2014), such as I found. The lack of response in carbon range suggests that changes in food-chain length are more substantial than changes in trophic breadth for freshwater food webs, implying that the resource base is not changing with abstraction flow loss, but trophic interactions are altered.

Contrary to expectations, I found no evidence suggesting there was an additional interaction of distance from abstraction point with decreasing local flow, or whether observations were upstream or downstream of the abstraction for any of my fish assemblage or food web characteristic metrics. I expected that distance from the abstraction would be more important for fish assemblages downstream where groundwater recharge would mitigate flow loss in the furthest downstream reaches. However, distance from the abstraction point was included as a variable in all my models to incorporate the spatial structure of my study design.

Implications

Many parts of the world are facing increasing demand for water for agricultural and municipal purposes and increasing modification of rivers (e.g., New Zealand's eastern coast, Western United States; Falke et al. 2011; Booker 2018), compounded by less precipitation, higher air temperatures, and shrinking groundwater tables due to anthropogenic development and climate warming (Malmqvist & Rundle 2002; Vörösmarty et al. 2010; Woodward et al. 2010; Duncan et al. 2016). To balance economic needs and environmental concerns, water managers need to assess the ecological outcomes of providing additional environmental flows at the cost of reducing irrigation allocations (Bunn & Arthington 2002; Poff et al. 2010; Horne et al. 2017). While there is no consensus on the development of general, transferable relationships between water abstraction and ecological responses, there is suggestion that greater alteration to flow regimes increases the risk of ecological change (Poff & Zimmerman

2010). Supporting this, my results show that small-scale surface water abstractions can significantly affect fish assemblages, depending on the proportion of flow removed. Such changes should be investigated further at broader geographic and temporal scales (and in terms of multiple compounding abstractions) to determine minimum flows and maximum allowable abstraction rates in rivers to balance the need to preserve endangered native fish species and sensitive recreationally-valued introduced species, such as brown trout, to ensure fish assemblages and aquatic communities do not collapse as a result of water abstraction.

In light of my results showing that even small abstractions can affect fish assemblages, freshwater conservation and restoration efforts, typically occurring at local spatial scales (Wohl et al. 2005), could be more effective if they were concentrated at strategic locations (e.g., abstraction points) within the catchment for greatest ecological outcome. In addition, managers of water resources need to consider the proportion of river flow abstracted as a parameter in addition to a set water volume (Benda et al. 2011). The identification of biologically meaningful abstraction conditions for management or restoration would help to identify target locations for restoration or conservation (Booker 2018).

There is some evidence from my findings, and from other studies, that suggest loss-of-flow can be beneficial to small-bodied native fishes vulnerable to trout predation and competition (Leprieur et al. 2006); assuming river connectivity is retained for the benefit of migratory species (e.g., longfin eels and torrentfish). At first sight this might suggest that management incorporating existing water abstractions could facilitate areas of refuge for native fishes and enhance co-occurrence between vulnerable native species and economically-important and recreationally valued introduced species (Chen & Olden 2017). However, this would only be appropriate for cases where a native species or population is under threat of extirpation in a homogenous environment, because natural environmental

heterogeneity (e.g., streams with flooding disturbance or water temperatures outside of trout-preferred ranges), already provides refugia for native taxa (Boddy & McIntosh 2017; *N. Boddy 2017 unpublished data*). Moreover, flow loss may still have detrimental effects on native fish, just less so than trout, so further investigation is required on the impacts of abstractions on native assemblages in the absence of invasive predators.

Given my findings, it is crucial to continue research in this area to produce scientifically defensible guidelines for water removal limits, the management of flow modification, and fisheries in regulated rivers (Poff & Zimmerman 2010). This should be done at the riverscape- scale (Ward et al. 1999), given the potential effects of multiple, compounding abstractions that are commonly installed. Finally, balancing economic interests and ecological values in river management is essential in light of impending climate warming and continuing human development worldwide (Horne et al. 2017).

Appendix 3A: Supplemental Table and Figures

Table 3A.1. Summary of habitat characteristics and fish assemblage metrics measured or calculated for four sampled water abstraction sites in Canterbury, New Zealand (averaged across 15 reaches within each stream). Discharge was measured on the day of sampling, maximum flow loss is the difference between the highest and lowest measured flow at any reach in the stream, wetted width represents the width of the flowing stream channel, and RDI (River Disturbance Index) scores the flood-proneness of the stream channel by a visual assessment of the bed and bank. See Table 1 for units and description of fish assemblage metrics.

Variable	Pudding Hill Stream	Taylors Stream	Limestone Creek	Kowai River
Discharge (m^3/s)	0.56	0.87	<0.01	0.32
Maximum flow loss (%)	85	57	58	100
Wetted width (m)	7.56	10.12	2.45	3.97
River disturbance index	104	97	65	116
Abundance (no./m)	41	83	124	48
Biomass (g)	564	801	156	224
Mass–abundance slope	-1.12	-1.03	-1.03	-1.07
Native-trout abundance ratio	6.79	15.54	N/A	33.63
Native-trout biomass ratio	1.34	5.56	N/A	4.19
Food-chain length	3.39	3.56	3.42	2.55
Carbon range	3.58	4.00	2.88	2.66
Maximum species diversity	3	5	2	4

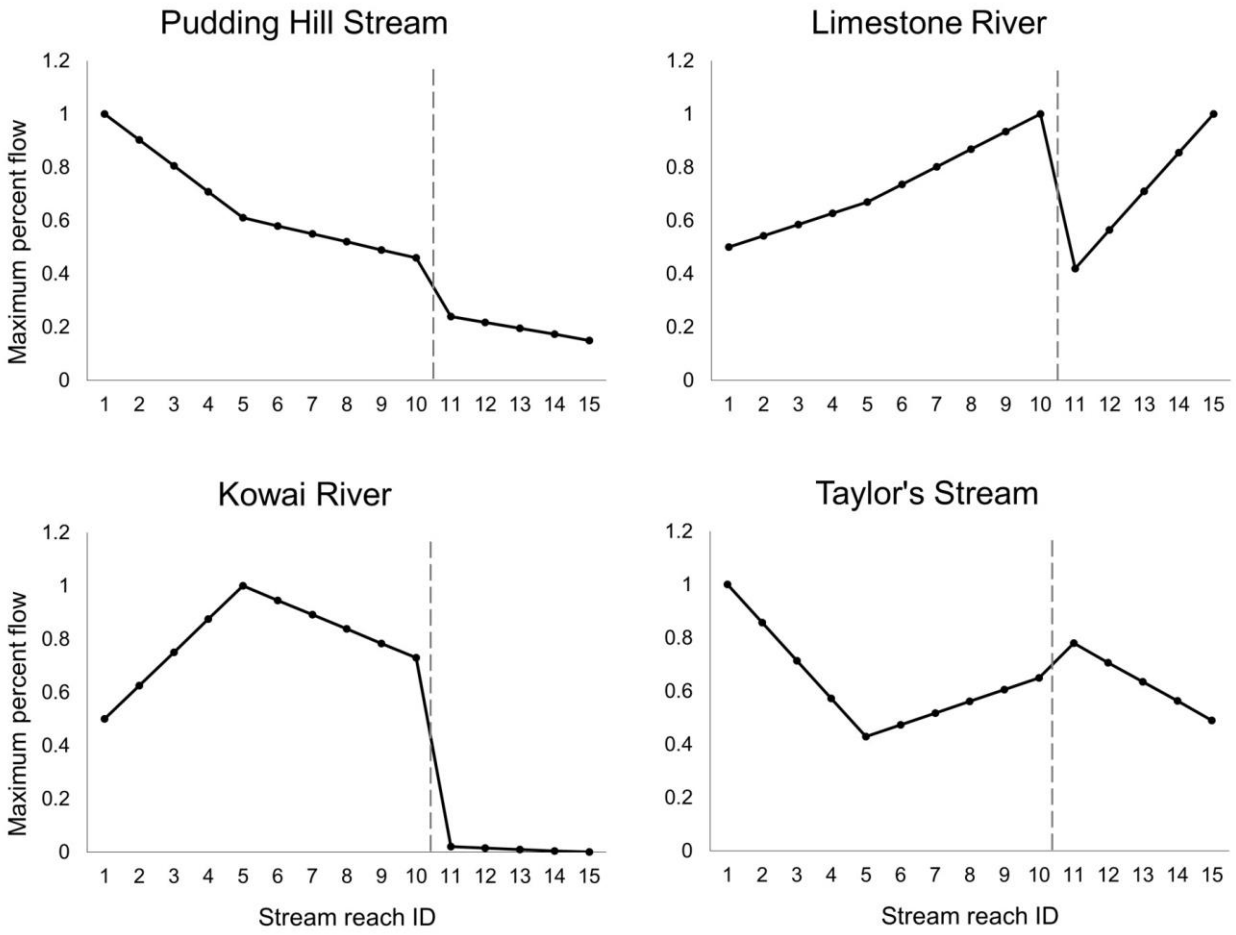

Figure 3A.1 Proportion of maximum stream flow for longitudinal sampling reaches around a surface water abstraction point. Reaches 1–10 were upstream of the abstraction and 11–15 were downstream. Values for reaches 2–4, 6–9, and 12–14 for all sites are interpolated discharge. The dashed vertical line denotes the abstraction point.

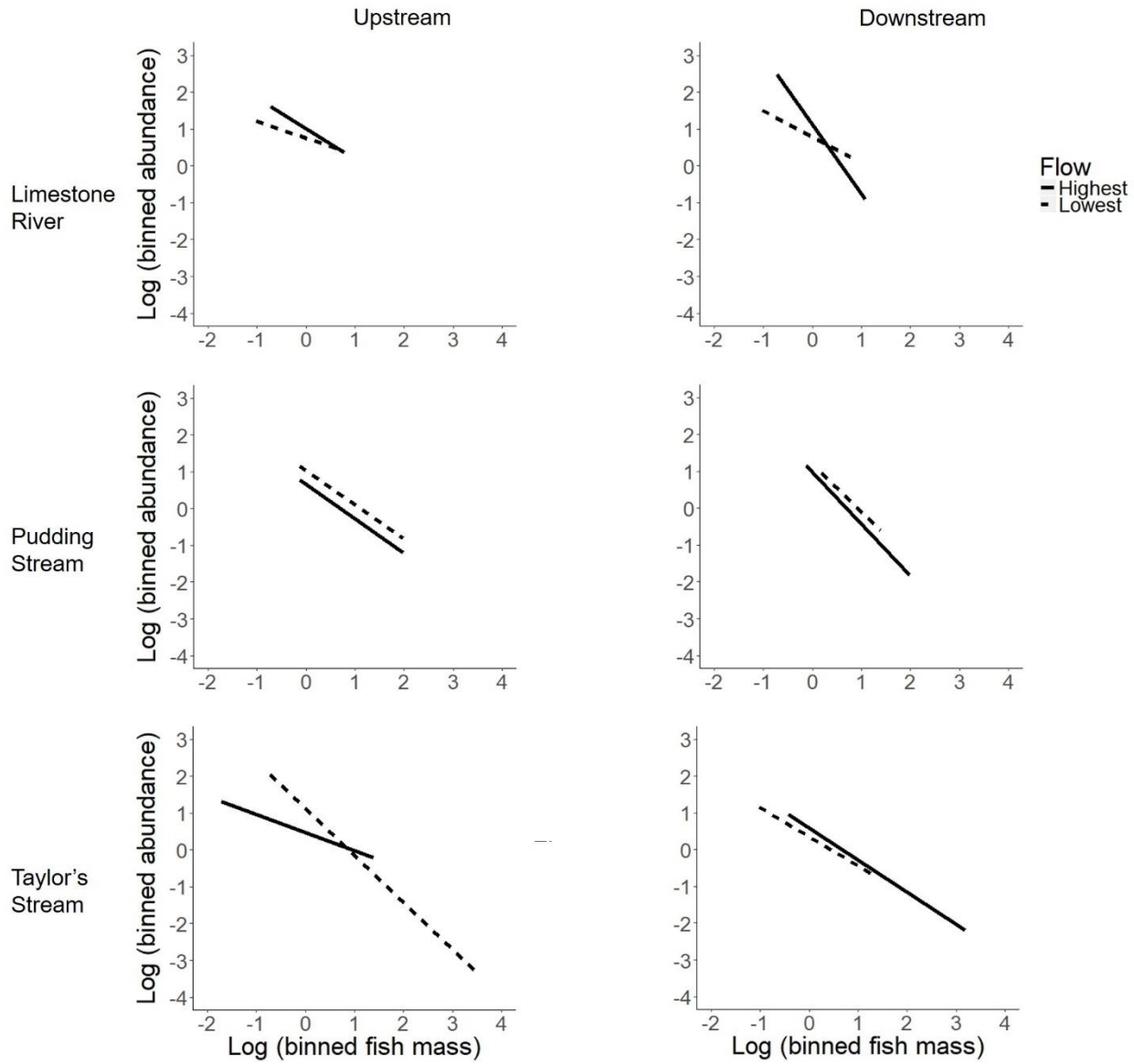

Figure 3A.2 Mass–abundance relationships for stream reaches with the lowest (dashed lines) and highest (solid lines) proportion of maximum flow upstream (left-hand panels) and downstream (right-hand panels) of surface water abstraction sites with sufficient data (Kowai River excluded due to reaches with zero flow). Note the addition of a larger size class of fishes (line extends further to the right) for the downstream reaches with highest flow.

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Co-Authorship Form

Please indicate the chapter/section/pages of this thesis that are extracted from co-authored work and provide details of the publication or submission from the extract comes:

Chapter Four "Variable influences on trophic position of temperate stream fishes associated with body mass, flood disturbance, and habitat size" was submitted to the journal "Freshwater Biology" for peer review and possible publication on 22 June 2018.

Fraley, K. M., Warburton, H. J., Jellyman, P. G., Kelly, D., & McIntosh, A. R. (2018). Variable influences on trophic position of temperate stream fishes associated with body mass, flood disturbance, and habitat size. Freshwater Biology, In review.

Please detail the nature and extent (%) of contribution by the candidate:

Kevin is the first author on this scientific article submitted for publication. He developed the study design with input from coauthors, undertook all fieldwork, labwork, and data analysis, and synthesized the findings into a peer-reviewed journal article. He wrote the first draft of the text and likely wrote 90% of the text as a whole. He also handled the entirety of the journal submission process and review. Supervisor Angus McIntosh reviewed and provided suggestions for improvements on several drafts of the article, and other coauthors reviewed at least one draft.

Certification by Co-authors:

The undersigned certifys that:

- The above statement correctly reflects the nature and extent of the PhD candidate's contribution to this co-authored work
- In cases where the candidate was the lead author of the co-authored work he or she wrote the text

Name:	Signature:	Date:
Angus McIntosh		23/7/18

Chapter Four

Variable influences on trophic position of temperate stream fishes associated with body mass and habitat size

Canterbury galaxias and upland bullies captured from the Kowai River, a study stream from this Chapter.

Abstract

In animals with indeterminate growth such as predatory fishes, mouth size is related to, and increases with, body mass of the organism. As fishes grow in body size they can consume larger-bodied prey items at potentially higher trophic levels. Therefore, body size may be connected to trophic position. Trophic position (TP) is useful for describing energy flow between biota, giving a more comprehensive picture of aquatic food webs, but current methods for deriving TP, typically diet studies or nitrogen stable isotope analysis, are time consuming and expensive, and the factors influencing the body size–trophic position relationship are unclear. Using mixed–effects linear models, I tested fish body mass as a predictor of TP for 8 species of temperate freshwater fish (n = 968 total individuals) sampled from 110 stream reaches, and evaluated habitat factors (flood disturbance and stream size) likely to affect trophic structure of stream fish assemblages. Supporting ecological theory, but contrasting with some fish body size–trophic position findings in marine and tropical environments, I found that trophic position was significantly correlated with body size across all species, and stronger within-species relationships were present for most taxa. Additionally, increased stream size negatively influenced the average trophic position of non-native salmonids, while the trophic position of native shortfin eels was higher in large streams. However, spatial factors included in models as random effects explained the majority of variance in trophic position for most species. Thus, fish body size and habitat factors are linked to stream fish trophic position, but researchers will need to account for other unmeasured spatial factors that explain variation in the TP of fishes to make accurate inferences about trophic height.

Introduction

In predatory or omnivorous animals that undergo indeterminate growth (e.g., insects and fishes; Charnov & Berrigan 1991), prey size is limited by mouth size (i.e., gape size limitation; Scharf et al. 2000). Thus, as organisms like fish grow, they are able to eat larger prey items. Since larger prey potentially occupy higher trophic levels (Arim et al. 2010; Riede et al. 2011), as predators get larger there may be a corresponding increase in their trophic position; and the largest-bodied organisms in an aquatic ecosystem typically sit atop food webs in aquatic ecosystems (Woodward et al. 2005). This theory has variable support across species for marine and tropical freshwater fishes through diet and stable isotope studies: either there is no relationship between body size and trophic position (slope of zero; Layman et al. 2005) or a positive relationship of approximately 0.34*body mass with TP (Jennings et al. 2001; Arim et al. 2010). However, much remains to be learnt about the key drivers of these trophic relationships in aquatic systems.

Body size–trophic position relationships have not been investigated for temperate freshwater fishes, which have unique life history strategies and can be subject to harsh environmental conditions. Moreover, different fish taxa exhibit different body forms, feeding strategies, and energetic needs. Thus it may be expected that relationships between body size and trophic position would be strongest within-taxa, if a sufficient range in body sizes was assessed. They might also differ between species given varying trophic niches for life histories and that habitat factors will affect trophic position differentially among species. Because assessing the trophic position of organisms is useful for understanding energy flow and mechanisms controlling food-web structure, quantifying these relationships will contribute to ecological knowledge. Additionally, if a reliable link can be established between the body sizes of fishes and their trophic positions, body size could be used to infer TP in food-web studies (Jennings et al. 2001).

Understanding how habitat factors affect variation in the body size–trophic position relationship will also be useful for investigating effects of human habitat alteration on aquatic communities. Habitat conditions such as temperature and habitat size affect fish feeding behaviour, diet, energetic budgets, and trophic position (Post et al. 2000; Arim et al. 2007; McHugh et al. 2010), therefore it is likely that factors such as stream size, flood disturbance, productivity, and species composition would as well. For example, a fish living in a flood-prone diversity-poor stream where algal and invertebrate standing stock was regularly disrupted may have limited prey options, including fewer intermediate predatory invertebrates, and may feed at a lower trophic level when compared to a fish of the same size living in a productive spring creek with multiple, stable prey options. By comparison, a large predatory fish occupying a sizeable habitat containing multiple intermediate predators and higher prey diversity may feed at a higher trophic level because of the increased availability or abundance of prey at intermediate levels of the food web (McCann et al. 2015). Therefore, theorized relationships between fish body size and trophic position should change depending on habitat conditions and individual streams, or possibly even catchments. Thus, different locations would have unique patterns in body size–trophic position relationships because of different combinations of habitat conditions. Additionally, habitat conditions likely affect body size–trophic position relationships differently for each species via differing trophic niches and traits (Kidd et al. 2001; Romanuk et al. 2011). Thus, if trophic position is to be utilized to characterise energy pathways in aquatic food webs, the species-specific effects of physical habitat factors and stream spatial position on variance in fish body size–trophic position relationships need to be investigated and accounted for.

With considerations about species-specific body size effects and variance caused by habitat conditions on trophic position in mind, I hypothesized that a positive relationship between fish body size and stable isotope-derived trophic position would exist across all

species, despite some evidence to the contrary from previous research (*H1*). Trophic position was predicted to decline with increasing flood disturbance (*H2*) because of decreased trophic omnivory in harsher, flood-prone habitats. As habitats become larger in discharge, habitat size (possibly interacting with flood disturbance) was hypothesized to increase trophic position through increased productive space and diversity of prey (*H3*). Stream reach and catchment-specific spatial patterns were expected to modulate trophic position due to differences in unmeasured habitat characteristics and energy sources between streams (*H4*). Finally, species-specific body size–trophic position relationships were hypothesized to be stronger due to metabolic and morphologic characteristics specific to certain taxa (*H5*).

Methods

Study Site

I sampled 110 reaches within 57 wadeable streams in seven river catchments of Canterbury, New Zealand during January-April of 2016 and 2017. These streams were selected *a priori* based on knowledge of conditions at potential sites, cursory site visits, information from the New Zealand Freshwater Fish Database (McDowall & Richardson 1983), and satellite imagery to incorporate a wide gradient of hydrological disturbance (flood disturbance), discharge (habitat size), land cover (from pastoral to indigenous forest), and fish species diversity (including both native and introduced taxa). The breadth of habitat conditions contained within this diverse selection of sampling reaches allowed for high strength of inference. Lengths of sampling reaches were 13 m (n = 10), 20 m (n = 16), 30 m (n = 15), 35 m (n = 5), and 50 m (n = 66), a result of using samples from multiple investigations with slightly different methodology.

Habitat measurements

Habitat characteristics identified in previous studies as possible influences on New Zealand stream fish stable isotope metrics were measured at each reach (McHugh et al. 2012;

Chapter Two). Most notably, these included discharge (m^3 $s^{-1,}$ one measurement per reach as a proxy for habitat size) and river disturbance index (RDI, flood disturbance; Pfankuch 1975). We chose discharge as our measure of habitat size because unlike commonly-used metrics such as cross-sectional area, discharge encompasses aspects of both volume and stream velocity, which can both be important drivers of fish assemblages in New Zealand streams (McIntosh 2000, McIntosh et al. 2018). While discharge at any one location is highly variable across time, we measured m^3s^{-1} at the same time as our fish sampling for each reach. For our flood disturbance metric, RDI was calculated by summing scores from 15 habitat assessment categories, with a lower score indicating a reach is less hydrologically disturbed (flood disturbance). Indicators measured for RDI included: stream bank slope, potential for erosion into channel, debris jam potential, bank vegetation cover, width/depth ratio, bank rock size, presence of obstructions or deflectors, evidence of channel cutting, gravel bar deposition, substrate angularity, substrate brightness, substrate packing, substrate size, % substrate scouring, and benthic algal cover. In my study catchments, RDI was highly correlated with other measures of flood disturbance such as bed movement (Jellyman et al. 2013).

Fish capture and processing

Fish captured at each reach using either single-pass (n = 85 reaches) or three-pass electrofishing (n = 27 reaches), depending on the dataset of origin. All fish species were identified and measured to the nearest 1 mm (fork length for salmonids and total length for other species), and a subsample of individuals representative of species diversity and body sizes within the reach were euthanized (if < 400 mm) or fin clipped for stable isotope analysis. Fin tissue was substituted for muscle tissue to facilitate non-lethal sampling to protect large-bodied fish (eels and trout) that are important to breeding populations for their species; Hanisch et al. 2010). Electrofishing was performed in a downstream direction using

a Kainga EFM 300 backpack electrofisher (NIWA instrument systems, New Zealand) generating 400–600V of pulsed DC current. Fish were euthanized with an overdose of anesthetic (AQUI-S™ 20E; AQUI-S New Zealand Ltd.) and frozen for later stable isotope processing in the laboratory.

Stable isotope preparation and analysis

Primary consumers (*Deleatidium* spp.) were collected with a kicknet at each sampling reach at the same time as fish samples were taken, and *Deleatidium* were frozen for transport back to the laboratory. This macroinvertebrate is ubiquitous in unimpacted New Zealand streams and was present across all sampling sites so was utilized as a baseline primary consumer to compare with fish for SI food-chain length analysis (McHugh et al. 2012), and I verified their suitability for most of the reaches in Appendix 4B (fish from outlying reaches were excluded from analyses). In the laboratory, *Deleatidium* from each reach were dissected, and the stomach contents and head removed to eliminate bias from the returned SI values (Lancaster & Waldron 2001). Composite *Deleatidium* samples were gathered from n = 20–100 individuals from each location (Post 2002). Fish were dissected and a portion of dorsal muscle tissue (or fin tissue) was extracted. Next, fish and invertebrate tissues were dried in an oven for at least 72 hours at 50° C. After removal from the oven, samples were ground into a fine powder using a mortar and pestle, with care taken to avoid contamination. Approximately 2 mg of powder from each sample was placed in 8 × 5 mm tin capsule, folded, and sent to the University of California–Davis Stable Isotope Facility for analysis through isotope ratio mass spectrometry (PDZ Europa 20-20; Sercon Ltd.).

The resulting nitrogen isotope ratios were used to calculate trophic position of the sample organism, using the following equation from Post (2002):

$$TP_{ij} = \lambda + (\delta^{15}N_{ij} - \delta^{15}Nbase_{j}) / \Delta, \qquad \text{(Equation 4.1)},$$

where $\delta^{15}Nbase_j$ is the mean baseline from reach j, λ is the trophic position of the baseline (primary consumer; 2), and Δ is the mean fractionation rate (3.4‰; Post 2002; McHugh et al. 2010). The fractionation rate of 3.4‰ is one used by several researchers in studies of similar aquatic environments, and while likely not accounting for the variation in fractionation rates among our species of interest, is the best available value. It was not necessary to correct fin clip SI values to muscle values for *S. trutta* and *O. mykiss* per McCarthy and Waldron (2000) and Hanisch et al. (2010), respectively, who found no significant differences between tissue types for these species. Corrections were available and were implemented for *Anguilla dieffenbachii* (Chapter Two), but no correction for *A. australis* was available in the literature, so regressions relating fin clip to muscle SI values were constructed from a subset of euthanized individuals as follows:

A. australis $\delta^{15}N_{corrected} = 0.9753 \times \delta^{15}N_{fin\ clip} + 0.1968$ (Equation 4.2; $R^2 = 0.98$; Figure 4A.1).

All *A. australis* fin clip SI values were corrected to muscle values for analysis as per Equation 4.2 (Jardine et al. 2005) before TP was calculated.

Data analysis

I evaluated the relationship between trophic position and fish mass (log_{10} transformed for linearity; g), and included additional predictor variables of species, discharge (habitat size), and RDI (flood disturbance). Collinearity of predictors was evaluated by calculating variance inflation factors (VIF; cutoff ≥ 5) and eliminated by pruning collinear variables, and a set of linear models was constructed for the response variable using the (lmer) function in R version 3.1.3 (Package 'lme4'; R Development Core Team 2016). A categorical variable 'Stream ID' unique to each reach sampled) was nested within a categorical variable 'Catchment ID' (representing the river catchment that the reach was located within) as a

random effect in the models to account for spatial and stream-network influences in the data. I chose not to include stream reach or catchment as main effects because the main relationship of interest was that between fish body mass and trophic position. However, the amount of variability in the data explained by reach and catchment effects was captured in the difference between the marginal R^2 (mR^2; variability explained by main effects) and conditional R^2 (cR^2; variability explained by fixed and random effects) reported for top models (Nakagawa and Schielzeth 2013).

Candidate models were built for fish body size and trophic position relationships pooled across species (for a subset of 6 species with sufficient sample size, $n = 921$ individuals), and later for individual species using an *a priori* approach to predictor selection. This included models with interactions between habitat size and flood disturbance, as observed for some New Zealand catchments by McHugh et al. (2010). All possible combinations of factors (fish body mass, habitat size, species, and flood disturbance), as well as combinations with an interaction term between habitat size and flood disturbance, were included in the candidate set. I used an information-theoretic approach to select the best models predicting trophic position given the data (Burnham & Anderson 2002). Top models were selected based on Akaike's Information Criterion (AIC) scores; those with the lowest AIC ($\Delta AIC < 5$) were considered top models. I averaged parameter estimates over models with $\Delta AIC < 5$ to address model uncertainty (Burnham & Anderson 2002; Posada & Buckley 2004), and ninety-percent confidence intervals for model–averaged parameters were calculated to evaluate whether parameters overlapped zero, to determine significance.

Results

Fish capture and processing

A total of 1,091 fish were sampled (Table 2), including Canterbury galaxias (*Galaxias vulgaris*), alpine galaxias (*Galaxias paucispondylus*), upland bully (*Gobiomorphus*

breviceps), shortfin eel, longfin eel, Chinook salmon (*Oncorhynchus tshawytscha*), rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), common bully (*Gobiomorphus cotidianus*), and European perch (*Perca fluviatilis*). Rainbow trout were not included in the pooled species analysis due to low numbers of individuals collected, but were evaluated in a species-specific manner. Following McHugh et al. (2010), Chinook salmon were similarly excluded from the pooled species evaluation because of possible retention of maternal marine-derived nitrogen in the tissue samples that would likely skew results. European perch and common bully were dropped from both the pooled and individual species analyses because of low across-site replicates, and fish from reaches that exhibited outlying *Deleatidium* spp. δ^{15}N–fish δ^{15}N values were excluded from analysis (Appendix A), leaving a remaining sample size of 921 individual fish for the final pooled species model set.

Table 4.1. Numbers and characteristics of fish species collected for stable isotope and body size analysis in Canterbury, New Zealand. * denotes species with a small sample size or low numbers of between-reach replicates, and [n] denotes native species.

Species	*n*	Mean length (mm)	Length range (mm)	Mean mass (g)	Mass range (g)	Mean trophic position
Anguilla australis [n]	45	246.6	75– 900	116.8	0.6– 1814	3.81
Anguilla dieffenbachii [n]	81	457.4	140– 1230	463.7	5– 5991	3.59
Galaxias paucispondylus [n]	33	78.0	59– 117	2.8	1.1– 9.0	3.31
Galaxius vulgaris [n]	236	74.6	34– 146	4.9	0.6–27.5	3.36
Gobiomorphus breviceps [n]	355	57.3	25– 110	3.2	0.2– 20.1	3.23
*Oncorhynchus mykiss**	13	266.8	40– 605	508.3	0.4– 2081	3.34
*Oncorhynchus tshawytscha**	19	67.7	44– 96	3.6	0.6– 10.3	3.13
Salmo trutta	270	140.1	30– 700	97.2	0.2– 3498	3.28

Body size and trophic position linkage across species

Examining body size–trophic position data across species, we found a clear effect of body mass on TP (Figure 4.1). Top models explaining fish trophic position ($\Delta AIC < 5$; the first three models in Table 4.2) included fish body mass, species ID, RDI, and habitat size, but no interaction terms (Table 4.2). While body mass (Figure 4.1) and species ID significantly affected TP, flood disturbance and habitat size did not.

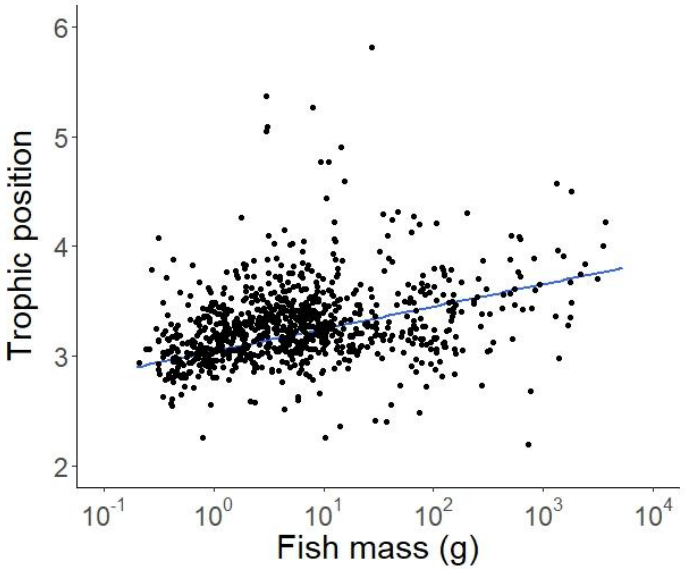

Figure 4.1. Scatterplot of the relationship between fish mass (g) and stable isotope-derived trophic position for *n* = 1020 fish (data for *O. tshawytscha*, *O. mykiss*, *G. cotidianus*, and *P. fluviatilis* were withheld as outlined in Section 3.1).

Marginal R^2 for the fixed effects of the top model was low ($mR^2 = 0.15$; Table 4.2), but the inclusion of random effects of stream reach and catchment explained much of the variability ($cR^2 = 0.58$), indicating that unmeasured stream reach and catchment characteristics (and their unique effects on fish diet and feeding behaviour) may be important along with body mass, flood disturbance, and habitat size in describing the trophic position of fishes generally. Despite finding an across-species relationship between body size and TP, I proceeded to construct and evaluate species-specific models to compare with the pooled model, and for practical use by freshwater scientists studying our species of focus.

Table 4.2. Summary of model–selection statistics for the top ten models (ranked by Akaike information criterion; AIC) relating log-transformed fish body mass (g), fish species, river disturbance index (RDI), and habitat size (discharge in $m^3 s^{-1}$) to trophic position for n = 921 fish in Canterbury, New Zealand streams. Top models are the first three that had ΔAIC <5. Abbreviations are as follows: L–L, the log–likelihood; ΔAIC, the difference in the Akaike information criterion value for a particular model compared with the top-ranked model; w_i, the AIC weight; E_r, the evidence ratio (i.e., w_{top} / w_i); K, the number of parameters, including the intercept and residual variance; $m R^2$, the marginal R^2 of the top model; and $c R^2$, the conditional R^2 of the top model. The full candidate set of models tested included all possible combinations of the factors and interactions. * denotes an interaction between predictors.

Model	L–L	AIC	ΔAIC	w_i	E_r	K	mR^2	cR^2
RDI, Species, Mass	-80.1	182.4	0.0	0.42	1.0	11	0.15	0.58
Species, Mass	-81.2	182.7	0.3	0.36	1.2	10	0.15	0.57
Habitat size, RDI, Species, Mass	-79.9	184.2	1.7	0.18	2.3	12	0.15	0.58
RDI, Species*Mass	-78.0	188.6	6.1	0.02	21.0	16	0.15	0.58
Species*Mass	-79.1	188.7	6.3	0.02	21.0	15	0.15	0.57
Habitat size, RDI, Species*Mass	-77.8	190.3	7.9	0.01	42.0	17	0.16	0.58
Mass	-142.0	294.0	111.6	0.00	–	5	0.07	0.49
RDI, Mass	-141.5	295.0	112.6	0.00	–	6	0.07	0.51
Habitat size, Mass	-141.8	295.6	113.2	0.00	–	6	0.07	0.49
Habitat size, RDI, Mass	-141.4	296.9	114.5	0.00	–	7	0.07	0.51

Table 4.3. Model–averaged parameter estimates ± SE, Z-statistic probability value (Pr(>|z|)), relative variable importance (R_i), and lower and upper 90% confidence intervals (CIs) for covariates (Table 4.2) relating log-transformed fish body mass (g), fish species, river disturbance index (RDI), and habitat size (discharge in $m^3 s^{-1}$) to trophic position of n = 921 fishes in Canterbury, New Zealand streams. Estimates are derived from averaging of models with ΔAIC < 5.

Covariate	Parameter estimate	Pr(>|z|)	R_i	Lower 90% CI	Upper 90% CI
Mass	0.20 ± 0.01	<0.01	1.00	0.18	0.23
RDI	- <0.01 ± 0.01	0.39	0.62	- <0.01	<0.01
Habitat size	-0.02 ± 0.03	0.57	0.18	-0.06	0.03
S. trutta	-0.27 ± 0.07	<0.01	1.00	-0.38	-0.15
G. paucispondylus	0.04 ± 0.07	0.54	1.00	-0.07	0.16
A. dieffenbachii	-0.21 ± 0.08	0.01	1.00	-0.34	-0.07
A. australis	0.08 ± 0.09	0.38	1.00	-0.07	0.23
G. breviceps	0.02 ± 0.07	0.76	1.00	-0.09	0.13

Species-specific relationships

Species-specific models relating fish body mass to trophic position included fish mass, RDI, and habitat size in top models (ΔAIC < 5) for all taxa, except *P. fluviatilis* (where sample size was small; Table 4.4). Fish mass was a significant positive predictor of trophic position for *G. vulgaris*, *G. paucispondylus*, *G. breviceps*, *A. australis*, *A. dieffenbachii*, and *S. trutta* (Table 4.5; Figure 4.2), and 90% confidence intervals for mass parameter estimates overlapped across these species (with slopes between 0.08 and 0.52). In contrast, fish mass was negatively correlated with TP for juvenile Chinook salmon, likely an artefact of fading maternal marine-derived nitrogen isotope signatures (slope between -0.94 and -0.46, Figure 4.3). Habitat size was a significant factor affecting trophic position of *A. australis*, *O. mykiss*, and *S. trutta* (although the effect was very close to zero for the latter, Table 4.5, Figure 4.4). Finally, flood disturbance did not significantly affect trophic position of any species (Table 4.5). Marginal R^2 was low (< 0.4) for TP of all species except *O. tshawytscha* and *O. mykiss*, but conditional R^2 was medium–high (> 0.45) for TP of all species except *A. australis*, again suggesting that unmeasured catchment and stream characteristics may play the biggest role in explaining variation in fish TP.

Table 4.4. Summary of model–selection statistics for top models (ΔAIC < 5) relating species-specific log-transformed fish body mass (g), river disturbance index (RDI), and habitat size (discharge in m^3 s^{-1}) to trophic position in Canterbury, New Zealand streams. Abbreviations are as follows: L-L, the log-likelihood; ΔAIC, the difference in the Akaike Information Criterion (AIC) value for a particular model compared with the top-ranked model; w_i, the AIC weight; E_r, the evidence ratio (i.e., w_{top} / w_i); K, the number of parameters, including the intercept and residual variance; $m R^2$, the marginal R^2 of the top model; and $c R^2$, the conditional R^2 of the top model. * denotes species with a small sample size or low numbers of between-reach replicates.

Species	Model	L–L	AIC	ΔAIC	w_i	E_r	K	mR^2	cR^2
G. vulgaris	Mass	-58.0	126.3	0	0.55	1.0	5	0.04	0.45
n = 235	Mass, RDI	-58.0	128.3	2.06	0.19	2.9	6	0.05	0.45
	Mass, Habitat size	-58.0	128.4	2.10	0.19	2.9	6	0.04	0.45
	Mass, Habitat size, RDI	-58.0	130.4	4.16	0.07	7.9	7	0.05	0.45
G. paucispondylus	Mass	12.2	-15.0	0	0.42	1.0	4	0.19	0.43
n = 33	Mass, Habitat size	13.3	-14.4	0.59	0.31	1.4	5	0.27	0.51
	Mass, RDI	12.4	-12.5	2.46	0.12	3.5	5	0.20	0.47
	Mass, Habitat size, RDI	13.4	-11.5	3.53	0.07	6.0	6	0.27	0.49
	Habitat size	10.0	-10.6	4.37	0.05	8.4	4	0.10	0.41
G. breviceps	Mass	44.2	-78.2	0	0.33	1.0	5	0.15	0.50
n = 320	Mass, RDI	45.2	-78.2	0.02	0.33	1.0	6	0.15	0.52
	Mass, RDI, Habitat size	45.8	-77.3	0.92	0.21	1.6	7	0.15	0.53
	Mass, Habitat size	44.3	-76.4	1.83	0.13	2.5	6	0.15	0.50
A. australis	Mass, Habitat size	-16.3	47.8	0	0.29	1.0	6	0.21	0.21
n = 33	Mass	-18.0	48.3	0.52	0.22	1.3	5	0.08	0.19
	Habitat size	-18.2	48.5	0.75	0.20	1.5	5	0.12	0.12
	Mass, RDI	-17.2	49.7	1.94	0.11	2.6	6	0.13	0.21
	Mass, Habitat size, RDI	-16.1	50.7	2.90	0.07	4.1	7	0.22	0.22
	RDI	-19.3	50.7	2.97	0.07	4.1	5	0.02	0.13
	Habitat size, RDI	-18.2	51.5	3.76	0.04	7.3	6	0.12	0.12
A. dieffenbachii	Mass	-37.7	86.4	0	0.42	1.0	5	0.11	0.45
n = 67	Mass, RDI	-36.8	87.0	0.56	0.32	1.3	6	0.16	0.47
	Mass, Habitat size	-37.7	88.8	2.34	0.13	3.2	6	0.11	0.45
	Mass, RDI, Habitat size	-36.8	89.5	3.06	0.09	4.7	7	0.16	0.47

S. trutta	Habitat size, Mass	18.4	-24.4	0.00	0.46	1	6	0.24	0.62
n = 233	Mass	16.5	-22.8	1.60	0.21	2.2	5	0.23	0.63
	Habitat size, mass, RDI	18.6	-22.6	1.79	0.19	2.4	7	0.24	0.62
	RDI, mass	17.3	-22.2	2.18	0.15	3.1	6	0.24	0.63
*O. tshawytscha**	Mass	3.37	4.11	0	0.58	1.0	4	0.43	0.84
n = 19	Mass, RDI	4.31	5.99	1.87	0.23	2.5	5	0.66	0.86
	Mass, Habitat size	3.47	7.67	3.55	0.10	5.8	5	0.41	0.83
	Mass, RDI, Habitat size	5.20	8.60	4.48	0.06	9.7	6	0.75	0.86
*O. mykiss**	Habitat size	3.49	6.02	0	0.42	1.0	4	0.41	0.85
n = 13	Mass	2.64	7.72	1.70	0.18	2.3	4	0.20	0.88
	Mass, Habitat size	5.24	8.10	2.07	0.15	2.8	5	0.66	0.88
	Mass, RDI	4.60	9.37	3.35	0.08	5.3	5	0.78	0.78
	RDI	1.76	9.48	3.46	0.07	6.0	4	0.06	0.86
	Habitat size, Mass, RDI	7.86	10.29	4.26	0.05	8.4	6	0.87	0.87

Table 4.5. Model–averaged parameter estimates ± SE, Z-statistic probability value (Pr(>|z|)), relative variable importance (R_i), and lower and upper 90% confidence limits (CLs) for covariates (Table 4.2) relating species-specific log-transformed fish body mass (g), river disturbance index (RDI), and habitat size (discharge in m^3 s^{-1}) to trophic position in Canterbury, New Zealand streams.. Estimates are derived from averaging of models with ΔAIC < 5. * denotes species with a small sample size or low numbers of between-reach replicates.

Species	Covariate	Parameter estimate	Pr(>|z|)	R_i	Lower 90% CI	Upper 90% CI
G. vulgaris	Mass	0.165 ± 0.042	<0.01	1.00	0.095	0.235
	RDI	0.001 ± 0.001	0.81	0.26	-0.003	0.003
n = 235	Habitat size	-0.005 ± 0.045	0.91	0.26	-0.080	0.070
	Mass	0.313 ± 0.116	0.01	0.95	0.116	0.511
G.	Habitat size	-0.047 ± 0.032	0.15	0.44	-0.101	0.007
paucispondylus	RDI	-0.0003 ± 0.001	0.83	0.20	-0.003	0.002
n = 33						
	Mass	0.233 ± 0.119	<0.01	1.00	0.189	0.277
G. breviceps	RDI	-0.002 ± 0.001	0.12	0.54	-0.004	0.001
	Habitat size	0.023 ± 0.027	0.41	0.34	-0.022	0.068
n = 320						
A. australis	Mass	0.171 ± 0.088	0.06	0.69	0.020	0.321
	Habitat size	0.242 ± 0.115	0.04	0.60	0.046	0.438
n = 33	RDI	0.004 ± 0.006	0.48	0.29	-0.006	0.015
A. dieffenbachii	Mass	0.259 ± 0.089	<0.01	1.00	0.111	0.408
	RDI	0.006 ± 0.004	0.15	0.43	-0.001	0.012
n = 67	Habitat size	0.023 ± 0.116	0.85	0.23	-0.172	0.217
S. trutta	Mass	0.197 ± 0.020	<0.01	1.00	0.164	0.231
	Habitat size	-0.06 ± 0.031	0.06	0.64	-0.107	-0.006
n = 233	RDI	-0.001 ± 0.001	0.41	0.34	-0.003	0.001
O.	Mass	-0.699 ± 0.136	<0.01	1.00	-0.938	-0.461
	RDI	0.006 ± 0.003	0.10	0.30	0.0002	0.0121
*tshawytscha**	Habitat size	-0.065 ± 0.089	0.50	0.17	-0.221	0.090
n = 19						
*O. mykiss**	Mass	0.154 ± 0.085	0.09	0.48	0.006	0.301
	Habitat size	-0.678 ± 0.284	0.04	0.65	-1.195	-0.161
n = 13	RDI	-0.011± 0.006	0.15	0.21	-0.022	0.001

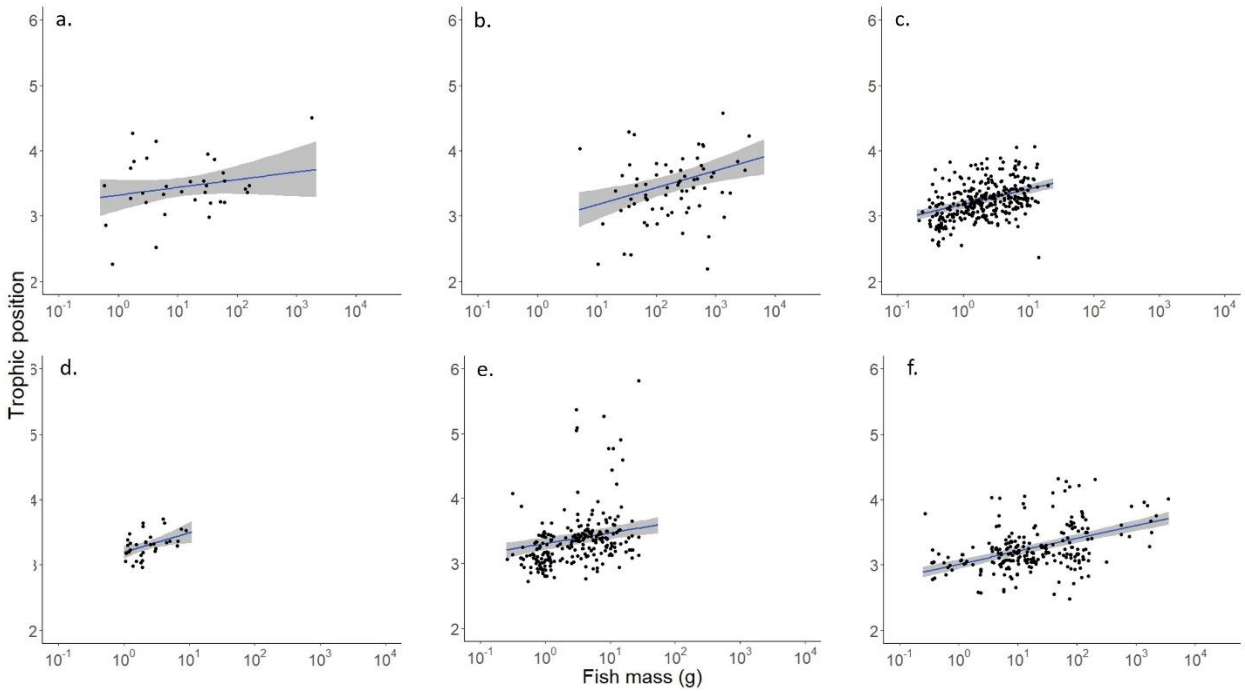

Figure 4.2. Raw data scatterplot and significant fitted model–averaged relationships (lines) between body mass (grams) and stable isotope-derived trophic position for (a) shortfin eel, (b) longfin eel, (c) upland bully, (d) alpine galaxias, (e) Canterbury galaxias, and (f) brown trout. Grey bands denote 90% parameter confidence intervals for model fit from Table 4.5, and are constrained near to the range of body size sampled for each species.

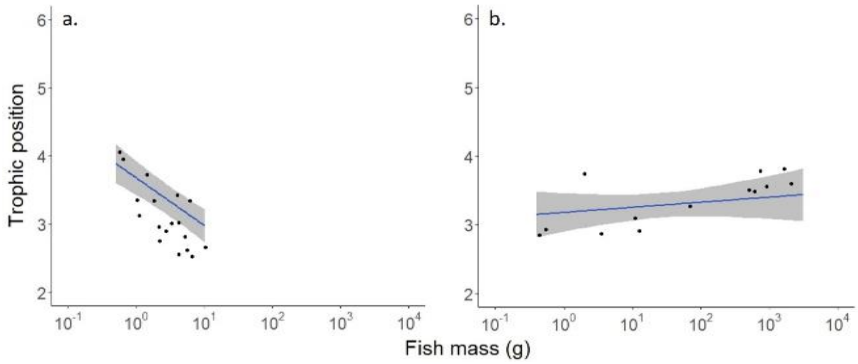

Figure 4.3. Scatterplot and fitted model–averaged relationship (lines) between body mass (g) and stable isotope-derived trophic position for juvenile Chinook salmon (a) and rainbow trout (b). The grey band denotes a 90% parameter confidence interval from Table 4.5. Note that predictions and confidence intervals are not robust for rainbow trout due to low sample size

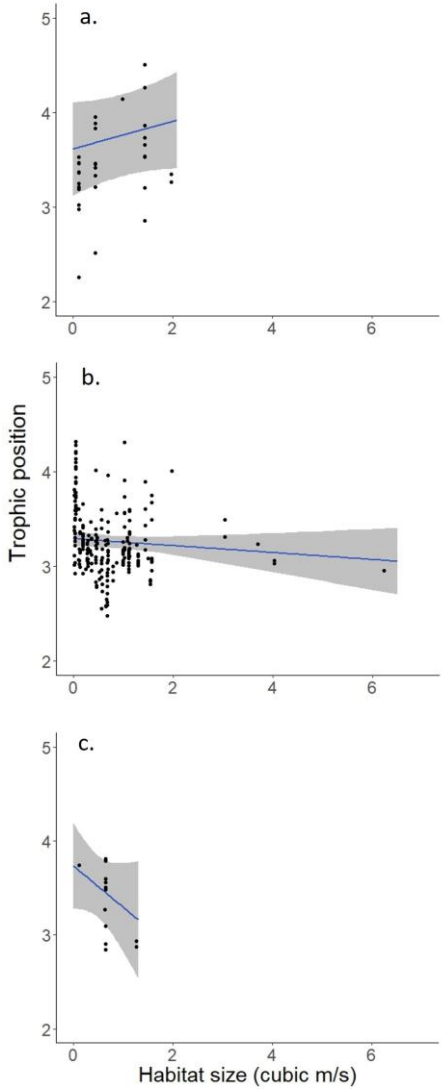

Figure 4.4. Raw data scatterplot and significant fitted model–averaged relationships (lines) between habitat size and trophic position for shortfin eel (a), brown trout (b), and rainbow trout (c). Grey bands denote 90% parameter confidence intervals from Table 4.5. Note that predictions and confidence intervals are not robust for rainbow trout due to low sample sizes.

Discussion

Some ecological theory and studies conducted on marine and tropical fishes suggest there is an across-species positive relationship between body size and trophic position (Woodward et al. 2005; Arim et al. 2010), and our findings corroborated this link overall for temperate fishes. Additionally, as expected, body mass-TP relationships were stronger when examined within-species in most cases, likely due to unique energetic demands, body type, and feeding strategies for each taxa. Additionally, habitat size did affect the relationship between fish body size and TP for some species, but unmeasured spatial and geographic organization of streams may be more important in explaining the variation in fish trophic position than body mass or habitat size. Thus, complex relationships involving fish species, body mass, habitat factors, and stream spatial patterns underpin changes in trophic height (i.e., the range in trophic position that a single species may attain), which we outline below.

Trophic position and body size relationship across species

Firstly, there was evidence of a relationship between fish mass and trophic position when assessed across all species, following what we expected in *H1*. This is in contrast to findings of Jennings et al. (2001) and Layman et al. (2005), who found non-significant or weak relationships for marine and tropical fishes across species, but aligned with Arim et al. (2010) who observed a positive correlation across four species of killifish. In my study, this relationship was evident despite the diversity of body types and life histories of fishes present at my sites, ranging from anguilliform (eels) to fusiform (trout), and including benthic as well as drift feeders (Romanuk et al. 2011). Fishes with different body shapes have dissimilar energetic needs because locomotion, feeding, and resting behaviours require different amounts of effort depending on the habitats each taxa prefers to occupy (Webb, 1984), which may explain why some researchers have not found a link between body mass and trophic position. Additionally, despite body size–gape size ratios varying among the groups of fishes

present in my stream reaches due to morphological dissimilarities, which likely affects the rate of growth required for different fishes to achieve higher trophic levels (Romanuk et al. 2011), the body mass-TP relationship held. Given all these likely differences, it is slightly surprising that there remained a consistent relationship between body mass and trophic position when all species were pooled.

Species-specific relationships

Species-specific body size-TP relationships existed for all the taxa I evaluated (supporting *H5*), although 90% parameter estimate confidence intervals for *O. mykiss* and *A. australis* nearly overlapped zero. The lack of strong evidence for the relationship in the latter two may be due to lower sample sizes for each. Confidence intervals for the slopes of the body size–trophic position relationship of *A. dieffenbachii* and *G. paucispondylus* overlapped the 0.34 slope value reported by Jennings et al. (2001), while CI's for the other species were similar but slightly lower than 0.34, indicating that there is a similar scaling relationship between body mass and trophic position to marine fishes. Between the species of fish I evaluated, the slope of the body size–TP relationship was similar, although there were differences in observed variability and y-intercept amongst taxa. However, while increased body mass did result in an increase in trophic position for some species, the explanatory power of mass in predicting TP was typically low (i.e., poor marginal R^2; exceptions: *O. tshawytscha* and *O. mykiss*), contrary to my expectation in *H5*. This indicates that body mass alone would be a poor proxy of trophic position, even within species and when habitat factors are accounted for (based on discussion of what constitutes a predictive model according to Mac Nally 2000).

Interestingly, while most species exhibited a positive relationship between mass and TP, the opposite was seen for juvenile *O. tshawytscha*, probably due to relict maternal marine signatures of enriched nitrogen isotopes passed on to juveniles in egg tissue (Mathisen et al.

1988). More than likely, if I had sampled larger *O. tshawytscha* (i.e., larger but not yet having moved to the ocean) I would have observed the relationship flatten and then become positive like that of the other fishes as the marine signature faded and the species began feeding higher in the freshwater food web as their body size increased.

Habitat size, flood disturbance, and spatial effects

While not interacting with fish body mass, the effects of flood disturbance (*H2*) and habitat size (*H3*) did significantly affect trophic position for some fish taxa. My findings follow those of McHugh et al. (2010) who found habitat size and disturbance both affected food-chain length in New Zealand streams. The significant influence of habitat factors on trophic level has also been reported for water temperature by Arim et al. (2007), lake size by Post (2000), and in the context of food-chain length by others (Sullivan et al. 2015; Kautza & Sullivan 2016). I found, as predicted by *H2*, that increased flood disturbance was associated with a decrease in trophic position for both *G. breviceps* and *G. cotidianus*, suggesting that the feeding behaviour, diet, and place in the food chain of these benthic-oriented native bully species was altered in streams that receive frequent and large floods. Jowett & Richardson (1994) found that bullies moved to sub-optimal habitats during floods, and their behaviour was more affected than other native and non-native species, potentially explaining this effect.

Interestingly, for both non-native trout species present at my stream reaches, decreased habitat size actually resulted in higher TP, conflicting with my prediction in *H3*. This indicates that these salmonids feed higher in the food web when relegated to smaller habitats. Possible explanations for this phenomenon could include increased piscivory by trout due to lower water velocity and fewer hiding places for prey fishes in small habitats (Ginetz & Larkin 1976; East & Magnan 1991; Woodford & McIntosh 2011), or increased availability of low-TP aquatic and terrestrial invertebrates in reaches with higher discharge (my proxy for habitat size; Kennedy et al. 2014). It is also possible that this correlation is not

biologically meaningful, as the parameter estimate for the effect was very close to zero for brown trout (-0.08) and the sample size was very low for rainbow trout (n = 13).

Taxa in which the body size–trophic position relationship were not affected by habitat size or flood disturbance, i.e., native eels and *Galaxias*, may be well-adapted to a range of these conditions, and thus their feeding behaviour, diet, and position in the food web is not greatly influenced by these factors (similar to findings regarding native fishes by Bestgen et al. 2017). Alternatively, there may be other habitat factors I did not measure that have greater influence on trophic position for these species (e.g., water chemistry, riparian land cover types other than pastoral cover, or terrestrial-source carrion food sources). Similar to fish body mass patterns, the inclusion of habitat size and flood disturbance in models did not greatly increase prediction power (i.e., marginal R^2 values high enough as discussed by Mac Nally 2000) of trophic position such that these measures could substitute for SI methods for most species.

Catchment effects and stream spatial structure, important factors influencing stream ecology (Isaac et al. 2014), when included as a random effect, explained a high amount of variance in fish trophic position data when compared to the influence of body mass, flood disturbance, or habitat size (most $cR^2 > 0.4$). This suggests plasticity of fish diets and trophic structure in habitats with differing physical conditions and prey bases, which would be typical of unique characteristics between different streams or catchments. This also suggests that there are other habitat factors in addition to fish mass, flood disturbance, and habitat size, differing among streams and catchments (Richards et al. 1996), that drove the majority of variation in fish trophic position. Thus, while researchers can expect that fish body size will increase positively with trophic position at any sampling site, the relationship will likely be weak and may be substantially different from a nearby stream if it differs markedly in size or disturbance regime.

Implications and recommendations

We have shown that body mass significantly affects the trophic position of fish species that we sampled in temperate streams, backing up ecological theory that hypothesizes a link between body size and TP in animals with indeterminate growth (Woodward et al. 2005). We have shown that this relationship can be present across multiple species, even though these taxa differ greatly in body shape, life history, and indigenousness. Based on my findings, if future researchers can illuminate the missing habitat factors and stream spatial attributes that contributed to high predictive power as captured by my nested Stream and Catchment ID variables as a random effect, then fish body mass in tandem with these attributes could be substituted for time consuming and expensive (relative to diet methods) SI sampling to infer TP. These non-lethal techniques would be particularly helpful when studying endangered or vulnerable fishes (Sanderson et al. 2009; Cooke et al. 2012). Additionally, I have shown that the relationship between temperate fish body mass and trophic position is affected by habitat conditions, and can be highly variable between catchments and even neighbouring streams within a single ecoregion. Thus, if changes to stream habitat characteristics occur through natural or human perturbations, this may influence energy pathways and trophic levels of fishes. This could potentially be detrimental to aquatic ecosystems and cause trophic cascades. Finally, I recommend that future researchers explore the effect of habitat factors beyond the ones I investigated, along with a temporal component, to further fill the knowledge gap of how trophic position is determined in freshwater fishes over space and time.

Appendix 4A: *A. australis* fin clip to muscle tissue regression

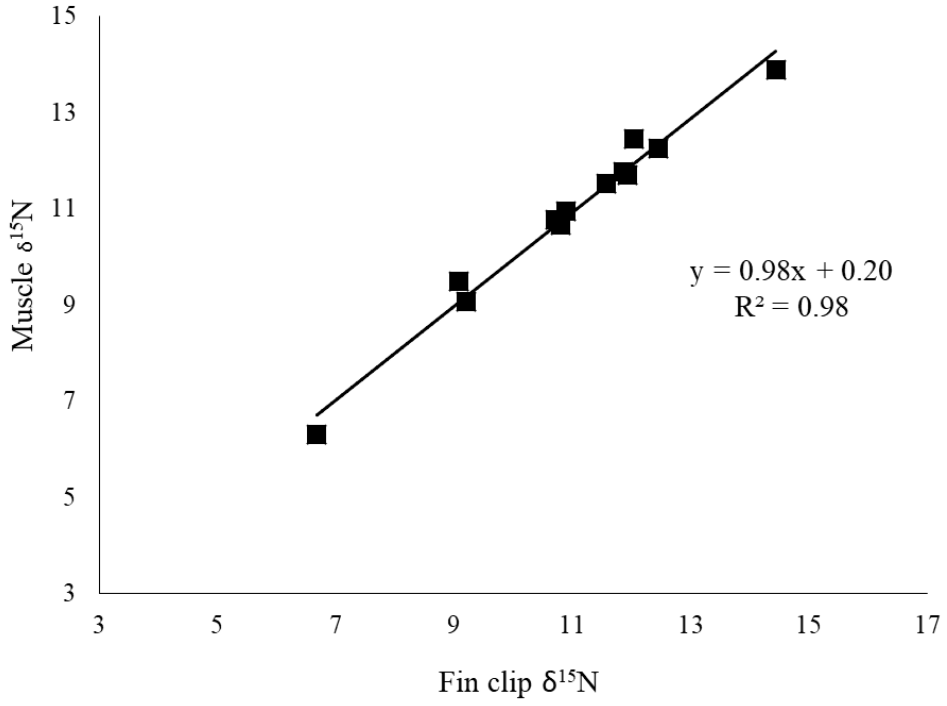

Figure 4A.1. Fin clip to muscle $\delta^{15}N$ correction regression for *A. australis* used to construct Equation 4.2.

Appendix 4B: Verification of stable isotope baseline

Introduction

Other stable isotope-based fish studies have been conducted in New Zealand using similar methods calculate trophic position and food-chain length (e.g., McHugh et al. 2010 and 2012). Specifically, a similar aquatic invertebrate baseline (primary consumer) was used, usually *Deleatidium* spp. mayflies, to standardise between-reach variability in isotope ratios. It is assumed that this baseline accurately reflects the food base of fishes and other biota that presumably feed upon them. While I found evidence in my study of biases and mismatches between fishes and this aquatic baseline, *Deleatidium* were a suitable SI baseline in most cases, as I discuss in this appendix.

Clapcott et al. (2012) found that nitrogen isotope ratios in biota can be affected by agricultural runoff, and I suspected that agricultural influences at a number of my reaches played a role in some of the outlying isotope values. Also, it is known that some fishes, when in habitats with low aquatic prey abundance or high allochthonous input, may rely more heavily on terrestrial food subsidies, and thus a non-aquatic or a mixed SI baseline is needed. This can be particularly true for non-native salmonids, which may utilize terrestrial insects for up to 44% of their diets (Cada et al. 1987; Edwards & Huryn 1995; Nakano & Murakami 2001). Conversely, the native taxa in my study area are benthic-oriented and feed mostly on aquatic prey items (e.g., *G. vulgaris* diet consisted of 6.6% terrestrial prey in one study; Cadwallader 1975; Sagar & Eldon 1983). Thus, it would be expected that the SI values would differ for taxa feeding from terrestrial ecosystems, particularly if the baseline was mismatched (e.g., aquatic invertebrate baseline used for a rainbow trout feeding exclusively on terrestrial cicadas).

Therefore, to evaluate land cover and species effects on stable isotope ratios and illuminate other possible biases, I teased apart some of these underlying relationships based on

terrestrial isotope values I measured (plants and invertebrates) and riparian land cover data available for my sampling streams.

Methods

I extracted riparian land cover data from The River Environment Classification (REC; Snelder & Biggs 2002) digital streamlayer, and the associated Freshwater Environments of New Zealand (FWENZ), which include attributes estimating a suite of landscape-scale (740 m average segment length) habitat characteristics derived from the New Zealand Land Cover Database for $n = 54$ of my sampling reaches. I chose to look at upstream pastoral riparian cover to evaluate the effect of agriculture on $\delta^{15}N$ isotope values. I ran simple linear regressions between the land cover predictor and both *Deleatidium* spp. baseline and mean fish $\delta^{15}N$ values for each reach, and used analysis of variance (ANOVA) F-tests to determine if agricultural land cover significantly affected SI values. I also ran linear models relating *Deleatidium* $\delta^{15}N$ values for $n = 54$ reaches to average $\delta^{15}N$ fish values by reach to evaluate the efficacy of *Deleatidium* as a baseline consumer for SI calculations. Finally, I tested correlations between fish $\delta^{15}N$ values and $\delta^{15}N$ values from composite terrestrial insect and composite terrestrial plant samples at $n = 29$ of my reaches to assess the possible contributions to fish diets from these pathways.

Results/Discussion

I found that both *Deleatidium* and fish $\delta^{15}N$ values were significantly affected by upstream pastoral cover (Figure 4B.1). Increasing upstream pastoral cover resulted in higher enrichment of $\delta^{15}N$ values, supporting Clapcott et al. (2012) findings that nitrogen ratios are affected by agricultural influences. However, because both fish and baseline consumer values responded similarly at most reaches (excluding the outlying reaches identified in Figures 4B.1 and 4B.2), *Deleatidium* were appropriate baseline organisms to use for nitrogen SI analysis in most streams.

Further-supporting my use of an aquatic baseline, I found that a relationship between *Deleatidium* $\delta^{15}N$ and average fish $\delta^{15}N$ was highly significant, and tightly related (R^2= 0.63; *p*-val = <0.01; Figure 4B.1). Conversely, there was poor explanation of fish $\delta^{15}N$ variability by terrestrial plant and invertebrate $\delta^{15}N$ values ($R^2 < 0.18$; Figure 4B.3). However, terrestrial invertebrate $\delta^{15}N$ was significantly correlated with fish $\delta^{15}N$, albeit with a slope close to zero. Additionally, certain stream reaches labelled in Figure 4B.1 (a) and Figure 4B.2 (Duck Creek, Okana River, Makerikeri River, Maori Lakes Outlet, and Lewis River at DOC campground) departed from expected relationship between fish and *Deleatidium* $\delta^{15}N$ and upstream pastoral cover (Fig 4B.1) and between *Deleatidium*–fish $\delta^{15}N$ (Figure 4B.2), likely due to the high agricultural influence at 4 of these 5 reaches). These outlying reaches were removed from body size–trophic position analyses. Thus, I conclude that while not perfect, *Deleatidium* are well-suited for use as an isotopic baseline in most of my study streams.

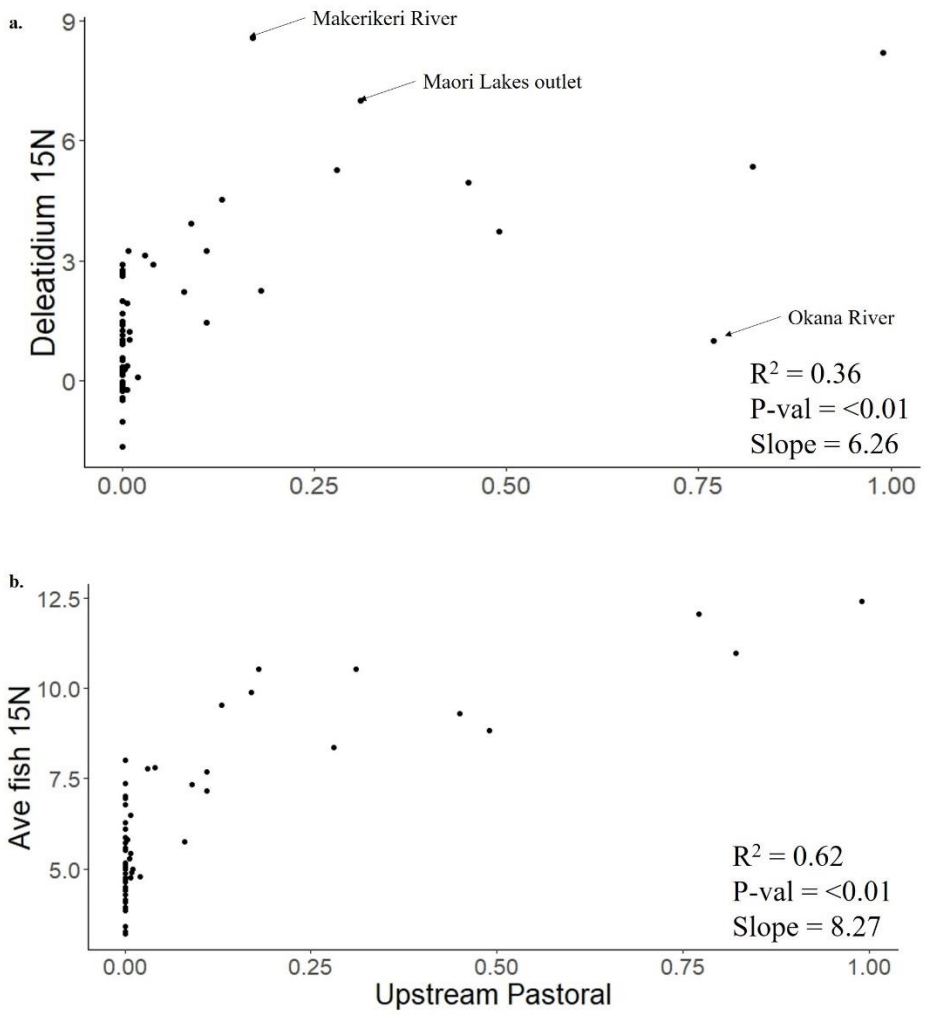

Figure 4B.1. Linear relationships between *Deleatidium* spp. (a) and average fish (b) $\delta^{15}N$ values to percent upstream pastoral riparian land cover by sampling reach (n = 54). Explanation of variance (R^2), Significance of the relationship (p-value), and the slope are noted in the lower right corners. Stream reaches outlying from the relationship are denoted by arrows and named, and are discussed in the appendix 'Results/Discussion.'

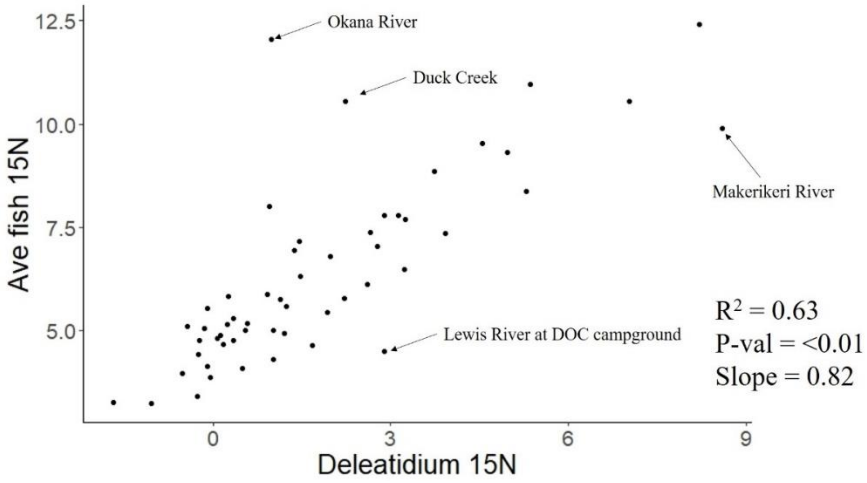

Figure 4B.2. Linear relationship between average fish $\delta^{15}N$ and *Deleatidium* spp. $\delta^{15}N$ values by sampling reach (n = 54). Explanation of variance (R^2), Significance of the relationship (p-value), and the slope are noted in the upper right corner. Stream reaches outlying from the relationship are denoted by arrows and named, and are discussed in the appendix 'Results/Discussion.'

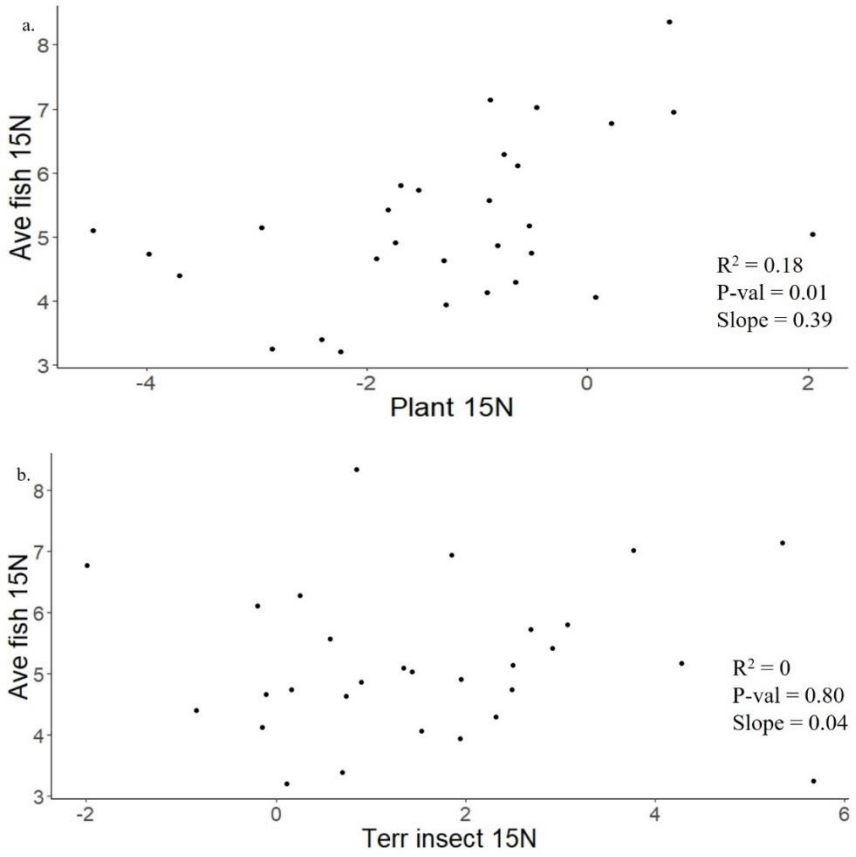

Figure 4B.3. Linear relationships between average fish and terrestrial plant (a) and terrestrial insect (b) $\delta^{15}N$ values by sampling reach (n = 29). Explanation of variance (R^2), Significance of the relationship (p-value), and the slope are noted in the lower right corners.

Chapter Five

Flood disturbance, habitat size, and land cover affect community biomass and stream fish trophic structure

An adult *Stenoperla* sp. stonefly found in the Lewis River, one of the study streams for this Chapter.

Abstract

A complementary analysis examining both stable isotope and biomass community components may be highly useful to stream managers, because it is unknown how these two responses may be influenced by habitat factors and perturbations. To test this, I characterised stable isotope-derived trophic height and biomass, including coarse allochthonous, algal, invertebrate, and fish components, for 27 New Zealand stream communities. Using piecewise structural equation modelling to test relationships between components, I found that increased habitat size did not affect the trophic height or biomass per unit area of large-bodied piscivorous fishes (non-native trout and native eels), although it did result in decreased biomass of small-bodied 'prey' fish taxa (primarily native benthic taxa), likely due to high water velocities in larger habitats rendering habitat less hospitable for small-bodied fishes. Additionally, native forest land cover was associated with increased instream allochthonous biomass, while pastoral cover correlated with high algal biomass and trophic effects, presumably from nitrate pollution. Finally, I found that flooding disturbance negatively affected both trophic height and biomass of large-bodied fishes, but did not affect small-bodied 'prey' fish taxa. Because flooding negatively affects large-bodied, culturally and economically important eels and trout, stream managers should consider lower harvest limits for streams that are flood-disturbed in order to conserve populations. Overall, describing stream trophic structure with complementary SI and biomass methods appears to be a useful approach for constructing an integrative picture of how abiotic and biotic habitat factors affect freshwater communities.

Introduction

Describing trophic structure and energy flow within lotic freshwater food webs is a useful tool for understanding the relationships between different components of a freshwater community (e.g., aquatic invertebrates and fishes; Bunn et al. 1999). Such an approach could allow river managers to identify threats and prevent them from causing food-web collapse or degradation (Wootton et al. 1996), particularly when sensitive native fauna or economically important fishes are involved.

Perturbation of freshwater food webs, if affecting the relationships between community components, could lead to unforeseen effects detrimental to community health (Borer et al. 2005; Garay-Narváez et al. 2013). Perturbations such as flood disturbance and change in habitat size are likely to affect maximum trophic height (food-chain length) of fish assemblages and aquatic communities (Sabo et al. 2010; McHugh et al. 2010; Chapter One), but many of the mechanisms driving these effects are still unclear, especially how habitat factors affect top predators (i.e., directly or indirectly through forcing changes in lower components of the food web such as invertebrates). Additionally, other variables like riparian land cover type have also been linked to effects on food-chain length (Chapter Three), but it is unclear what mechanisms influence this. For example, does pastoral cover affect fish trophic position indirectly through algae and invertebrate consumers, or are effects due to isotopic enrichment from nitrate pollution (Clapcott et al. 2012) influencing stable isotope (SI)-derived measures of trophic position? Therefore, understanding the mechanisms controlling freshwater trophic structure could give managers a tool for measuring and addressing effects of perturbations.

In addition to SI-derived trophic characteristics, describing the interrelation of components of community biomass (e.g., fishes or invertebrates) can be useful for understanding the trophic structure of aquatic communities (Brett and Goldman 1997), and

changes in the biomass of community components can signal perturbations to ecosystems (Mittelbach et al. 1995). For resource managers, biomass is a tangible measure that allows for easier justification to stakeholders for harvest limits or regulation of recreationally or commercially important fisheries (Pauly and Christensen 1995; Allen and Pine 2000; Lathrop et al. 2002).

Like SI-derived metrics, biomass of fishes, invertebrates, and other components are affected by flood disturbance in streams (Scrimgeour & Winterbourn 1989; Wootton et al. 1996). Biomass is also linked to other factors such as land cover type and habitat size (Stephenson & Morin 2009). Additionally, biomass of basal resources (periphyton) should be closely correlated with the biomass of primary consumers, prey fishes (small-bodied secondary consumers), and predators (large-bodied fishes) in either a bottom-up or top-down ecosystem model (Diehl 1992; Kaylor & Warren 2017). This is because community components are either boosting the resources available for higher trophic groups, or controlling lower trophic groups through predation (Power 1992). Allochthonous biomass (i.e., leaves, sticks, and other detritus) may also boost invertebrate biomass (Wallace et al. 2015), although the relationship is less-clear and depends on the composition of the aquatic invertebrate taxa present (Karlsson et al. 2015).

In a bottom-up ecosystem model, as I have used here, increased algal and allochthonous biomass should correlate with increased invertebrate biomass, because invertebrates utilize periphyton and allochthonous resources for food (Kaylor & Warren 2017). However, invertebrates vary in vulnerability to predators because of defenses (Covich 2010). Unarmoured invertebrates like Ephemeroptera and Plecoptera are palatable, and are frequently preyed on by fishes, potentially increasing small-bodied fish biomass, which are in-turn consumed by piscivorous fishes. Armoured invertebrates like Gastropoda and cased

Trichoptera are less-palatable for fishes (Wootton et al. 1996) and thus may be negatively correlated with fish biomass (Graham et al. 2015).

Both SI-derived metrics and biomass community component data can provide ecological knowledge and inform resource management (e.g., Mittelbach et al. 1995), and I expect that when utilized complementarily these two responses may yield even better understanding of mechanisms driving community structure. Specifically, knowledge of SI-derived trophic height can lead to recognition and mitigation of negative effects (e.g., trophic cascades) on freshwater ecosystems (Borer et al. 2005; Ellis et al. 2011; Garay-Narváez et al. 2013), but may not be particularly useful for setting biomass-based harvest limits for fisheries. On the other hand, knowledge of relationships between community components in a biomass context can help managers set harvest limits for fisheries, but may be less helpful for predicting trophic height and food-chain length (Mittelbach et al. 1995). Using a combination of community SI-derived and biomass trophic data would potentially lead to better-informed management, regulation, mitigation, and rehabilitation actions for stream managers. A direct, integrative comparison between equivalent components of SI-derived trophic structure and community biomass has not been previously investigated in freshwaters.

Thus, my specific objectives were to: 1) characterise and identify controls on SI-derived trophic height and community biomass in stream ecosystems of Canterbury, New Zealand using structural equation modelling, and 2) compare SI-derived trophic height and community biomass models to elucidate mechanisms determining trophic structure for ecological inference and to inform management action. I hypothesized that flood disturbance would negatively affect SI-derived trophic height and community biomass values for fishes and invertebrates (*H1*), that increased habitat size would positively affect fish SI-derived trophic height and fish biomass per unit area (*H2*), and that agricultural and native forest land cover would influence both SI-derived metrics and biomass of basal and secondary

community components (*H3*). More details of my specific predictions and the organisation of my structural equation models are provided in Appendices 5A and 5B.

Methods

Study site

I sampled twenty-seven wadeable stream reaches in the Ashburton/Hakatere (8 reaches), Ashley/Rakahuri (8), Waiau (8), Okana/Wairewa (1), Selwyn (1), and Waimakariri (1) River catchments of Canterbury, New Zealand (Figure 5.1). These streams were selected *a priori* based on site visits, the New Zealand Freshwater Fish Database, and satellite imagery to equally represent three categories of flood disturbance (RDI; low, medium, or high; Pfankuch 1975) and three categories of discharge (habitat size in m^3/s; small, medium, and large). Each stream was sampled at up to two locations and over 50-m sections (termed reaches).

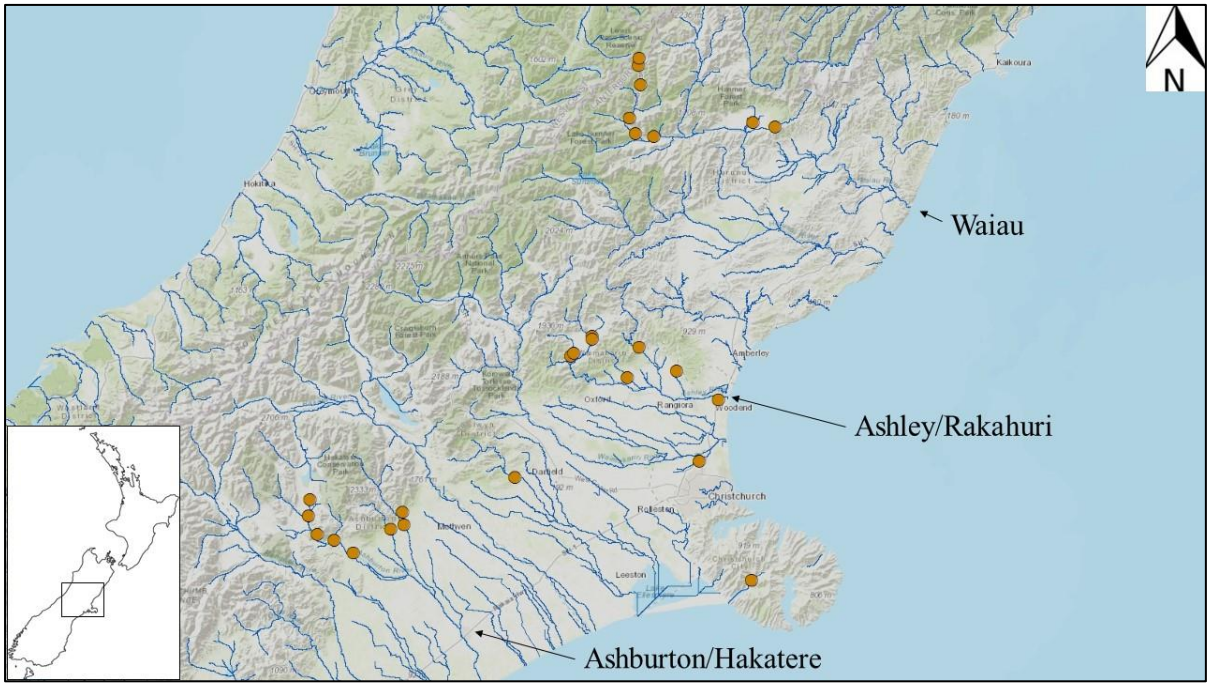

Figure 5.1. Main study river catchments (labelled) and sampling reaches (orange points) in Canterbury, New Zealand.

Habitat measurements

Because flood disturbance (RDI) and habitat size (discharge) were identified in previous studies as important influences on stream trophic dynamics (McHugh et al. 2010), these were measured at each reach. See Chapter One Methods section for an explanation of RDI and discharge calculations. Additionally, for each reach, I extracted two variables from the Freshwater Environments of New Zealand (FWENZ) digital streamlayer (Booker 2010; Leathwick et al. 2008) that I considered most-likely to influence primary productivity and nitrogen stable isotope ratios of biota (% upstream catchment pastoral cover) and allochthonous input (% upstream catchment native forest cover) as identified in Chapter Four and Chapter Two, respectively.

Invertebrate, periphyton, and coarse allochthonous biomass

Estimates of coarse allochthonous carbon and periphyton biomass were calculated for each reach to capture the main energy pathways in streams. Coarse allochthonous carbon, hereafter referred to as simply 'allochthonous biomass,' included terrestrial-source leaves, sticks, and other organic debris, but did not include terrestrial invertebrates. Periphyton, hereafter referred to as 'algal biomass', included the biofilm present on streambed rocks. Algal and allochthonous pathways are important drivers of aquatic ecosystem productivity and energy availability, and thus should be included in integrative models of trophic structure (Bilby & Bisson 1992; Baxter et al. 2005). Aquatic invertebrates use both of these energy sources, and so invertebrate biomass provides an integrative measure of energy and availability to higher trophic levels. Thus, I quantified invertebrate biomass by taking three 0.1 m^2 Surber samples in random locations at each reach, and the contents were preserved in 95% ethanol. In the laboratory, samples were sieved through a 500-mm sieve, aquatic invertebrates were extracted under a magnifying lens and microscope (Nikon SMZ800), sorted into armoured (Gastropoda, cased Trichoptera, and Coleoptera) and unarmoured (all

others) taxa, counted, dried, and ashed to obtain ash-free dry mass (g) per m^2 of streambed following methods similar to Quinn & Hickey (1990). Sticks, leaves, grass, and other terrestrial-source material were also picked from sieved material, dried, and ashed to estimate allochthonous ash free dry mass (g) per m^2 similar to methods employed by Franca et al. (2009). Algal biomass was estimated by randomly collecting five fist-sized rocks from the streambed at each reach, scrubbing and rinsing periphyton onto glass filters (Whatman™ GF/C microfiber, 47 mm diameter) in the laboratory, drying and ashing the filters, and then calculating ash-free dry mass (g) per m^2 following methods of Biggs & Kilroy (2000).

Fish capture, processing, and stable isotope analysis

Fish were captured at each reach using three-pass electrofishing with push nets, dipnets, and downstream stop nets. Fish were identified and measured, and a subsample of individuals approximately representative of species diversity and body sizes within the reach were euthanized or fin clipped for stable isotope analysis. Electrofishing was performed using a Kainga EFM 300 backpack electrofisher (NIWA instrument systems, New Zealand) generating 400-600V of pulsed DC current, conducted in a downstream direction following McIntosh (2000). Fish were euthanized with an overdose of anesthetic (AQUI-S™ 20E; AQUI-S New Zealand Ltd.) and frozen for later stable isotope processing in the laboratory.

Primary consumers (*Deleatidium* spp.) were collected with a kicknet at each sampling site, and frozen for transport back to the laboratory. These have been previously utilized as baseline primary consumers to compare with fish for SI food-chain length analysis (McHugh et al. 2012), and have been evaluated for suitability as a baseline in Chapters Two and Four. *Deleatidium* samples were gathered from 20-100 individuals from each location, following the composite invertebrate sample protocol used by Post (2002). In the laboratory, *Deleatidium* from each reach were dissected, and the stomach contents and head were removed to eliminate bias from the returned SI values caused by the inclusion of invertebrate

dietary items (Lancaster & Waldron 2001). Fish were dissected and a portion of dorsal muscle tissue was extracted (or fin tissue was substituted for clipped individuals to facilitate non-lethal sampling; Hanisch et al. 2010). Next, fish and invertebrate tissues were dried in an oven for at least 72 hours at 50° C. After removal from the oven, samples were ground into fine powder using a mortar and pestle, with care taken to avoid contamination. Approximately 2 mg of powder from each sample was placed in 8 x 5 mm tin capsule, folded, and sent to the University of California-Davis Stable Isotope Facility for analysis through isotope ratio mass spectrometry (PDZ Europa 20-20; Sercon Ltd.). The resulting Nitrogen isotope ratios ($\delta^{15}N$) were used for the sample organism in models and corrected for fin clips using Equations 2.5 and 4.2 in Chapters Two and Four, respectively.

Data analysis

Stable isotope and biomass data for fishes were split into two categories: small-bodied individuals, which were likely non-piscivorous (subsequently referred to as 'prey fishes') and large-bodied piscivorous predators (subsequently referred to as 'predator fishes'). The predator fish category included salmonids >150 mm and eels > 380 mm in length reflecting likely switches to piscivory at these sizes (McIntosh 2000; Jellyman 2001). Prey fishes were designated as salmonids < 150 mm, eels < 380 mm, and all other taxa. Additionally, invertebrate biomass was split into 'armoured' taxa defended with a shell, case, or unpalatable exoskeleton and an undefended 'unarmoured' category, similar to groupings made by Wootton et al. (1996), reflecting differential vulnerability to predators and flooding disturbance of these two groups. The armoured group was comprised of Gastropoda, cased Trichoptera, and Coleoptera taxa, while unarmoured included Ephemeroptera, Plecoptera, Diptera, uncased Trichoptera, and Megaloptera species. However, predatory and non-predatory invertebrates were not separated due to laboratory time constraints and irrelevance in terms of palatability for fishes.

All biomass variables were standardised by m^2 of streambed, and some of these were also log-transformed for linearity and scaling purposes to meet analysis assumptions. I constructed two piecewise structural equation models (SEM) to reflect predicted relationships (Appendices 5A and 5B). I had a low number of sampling reaches (27) in relation to the number of possible predictors, so piecewise SEM modelling was ideal for my data, enabling me to avoid model overfitting problems that occur with traditional SEM (Lefcheck 2016). Models included endogenous variables, or those with predictors, also characterised as responses for 'component models' (See Table 5.1). In addition, exogenous variables, or variables without predictors (non-responses) were included. Models were structured and evaluated using the 'piecewiseSEM' package in R version 3.1.3 (R Development Core Team 2016). Collinearity of predictors within component models was assessed by calculating variance inflation factors (VIF; cutoff ≥ 5) and pruning collinear variables. Catchment and stream ID were used as a nested random effect in the models to account for spatial and stream-network biases in the data. Fisher's C test within the 'piecewiseSEM' package was used to evaluate appropriateness of the overall SEM model for $\delta^{15}N$ and biomass (p-val > 0.05 = valid model). Standardised model coefficient estimates and p-values for significance ($\alpha < 0.05$) for paths within the SEM were calculated using the 'sem.coefs' function. The amount of variability in the data explained by reach and catchment effects was captured in the difference between the marginal R^2 ($m R^2$; variability explained by main effects) and conditional R^2 ($c R^2$; variability explained by fixed and random effects) reported for each component model (endogenous variable) within the SEM (Nakagawa & Schielzeth 2013).

Results

Fish capture and processing

A total of 3,770 fish were analyzed for biomass calculations and 609 for stable isotope analysis in this investigation, including Canterbury galaxias (*Galaxias vulgaris*),

upland bully (*Gobiomorphus breviceps*), shortfin eel (*Anguilla australis*), longfin eel (*Anguilla dieffenbachii*), common bully (*Gobiomorphus cotidianus*), brown trout (*Salmo trutta*), and European perch (*Perca fluviatilis*). Torrentfish (*Cheimarrichthys fosteri*), inanga (*Galaxias maculatus*), and lamprey ammocoetes (*Geotris australis*) were included in biomass calculations but not SI analyses because of potentially confounding marine-derived isotopes in the tissues of these diadromous fishes (eels were exempted from exclusion because they spend many years in freshwater). Predator fish biomass per m^2 was greater than that of prey fish, averaged across all sites. Predator fish consisted of trout and eels (52% by abundance were non-native trout), while prey fish were predominantly upland bullies and Canterbury galaxias (77% were native taxa).

Habitat factors

Discharge of sampling reaches ranged from <0.01 to 6.22 m^3/s, consisting of streams with a trickle of flow to those that were hip-deep and had a strong current. RDI scores ranged from 49 to 132, which included stable spring creeks at the low end and unstable, flood-prone streams at the upper end. Thus, my study reaches covered a wide range of habitat size and disturbance. Algal biomass averaged 2.79 g/m^2 across sampling reaches, ranging from mountainous streams that were scoured nearly algae-free to some lowland, agricultural watercourses with thick mats of periphyton. Coarse allochthonous biomass was on average 3.01 g/m^2, and encompassed stream reaches with very little woody debris to those with large deposits of leaves and sticks. Percent upstream catchment pastoral land cover across sampling streams had a mean of 18%, with some streams in unaltered catchments and others in completely agriculturalised catchments (range 0-99%). Similarly, percent upstream catchment native forest averaged 22% and my streams ran the gamut between zero native vegetation in the catchment to those where the majority of the catchment consisted of indigenous bush (range 0-88%). Biomass of unarmoured invertebrates averaged 0.38 g/m^2

ash-free dry mass and ranged from only 51 individuals per m^2 in depauperate, flood-prone reaches to over 2400 individuals per m^2 in stable streams, while armoured taxa had higher biomass (0.43 g/m^2 across reaches) and ranged from 11 individuals per m^2 in harsh reaches to over 3300 individuals per m^2 in stable streams.

Community biomass SEM

A Fisher's C-test confirmed that the piecewise SEM model structure I tested for biomass (Figure 5.2) was appropriate for the data (*p*-val = 0.09, above the 0.05 cutoff value suggested by Lefcheck 2016). In order of specific hypotheses tested, model results showed flood disturbance (*H1*) significantly decreased predator fish and armoured invertebrate biomass (Table 5.1, Figure 5.3b-c), but did not markedly affect prey fish, unarmoured invertebrate, or algal biomass. Flood disturbance was associated with a direct negative effect on predator fish biomass, although it was mitigated by an indirect negative effect of disturbance on armoured invertebrates, which were negatively associated with predator fishes (i.e., more armoured invertebrates were associated with fewer large, piscivorous fishes; Figure 5.3f). Therefore, flooding was likely a key modulator of top predator diet and trophic pathways.

Increased discharge (habitat size; *H2*) was correlated negatively with prey fish biomass (Figure 5.3d), but did not affect predator fishes. Thus, streams with higher discharge supported fewer small-bodied fishes per unit area, but the same number of large piscivores per m^2, as small streams.

Table 5.1. Standardised component model results from the structural equation model for algal, allochthonous, invertebrate, and fish biomass (g/m^2) from sampling reaches of Canterbury streams. Parameter estimates relate to the magnitude of the predictor on the component model response, and *p*-values denote the significance of the predictor on the component model response (*p*-value cutoff < 0.05). Marginal (mR^2) and conditional (cR^2) R^2 are also reported.

Component Model	mR^2	cR^2	Predictor	Parameter	Standard	*p*-value
Predator Fish	0.41	0.41	Flood disturbance (RDI)	-0.77	0.20	<0.01
			Armoured invertebrate	-0.69	0.20	0.03
			Prey fish	0.30	0.18	0.12
			Unarmoured invertebrate	0.39	0.25	0.14
			Habitat size (discharge)	0.05	0.19	0.81
Prey Fish	0.19	0.19	Habitat size (discharge)	-0.49	0.20	0.03
			Unarmoured invertebrate	-0.19	0.29	0.53
			Flood disturbance (RDI)	0.09	0.24	0.70
			Armoured invertebrate	0.08	0.33	0.80
Armoured Invertebrate	0.31	0.41	Flood disturbance (RDI)	-0.58	0.24	0.03
			Allochthonous	-0.19	0.19	0.33
			Algal	0.02	0.23	0.94
			Pastoral cover	0.02	0.27	0.95
Unarmoured	0.09	0.09	Flood disturbance (RDI)	-0.30	0.29	0.32
			Allochthonous	-0.22	0.23	0.34
			Algal	0.21	0.27	0.45
			Pastoral cover	-0.24	0.33	0.48
Algal	0.43	0.43	Pastoral cover	0.57	0.20	0.01
			Flood disturbance (RDI)	-0.15	0.20	0.46
Allochthonous	0.20	0.20	Native forest cover	0.45	0.20	0.03
			Pastoral cover	-0.01	0.20	0.95

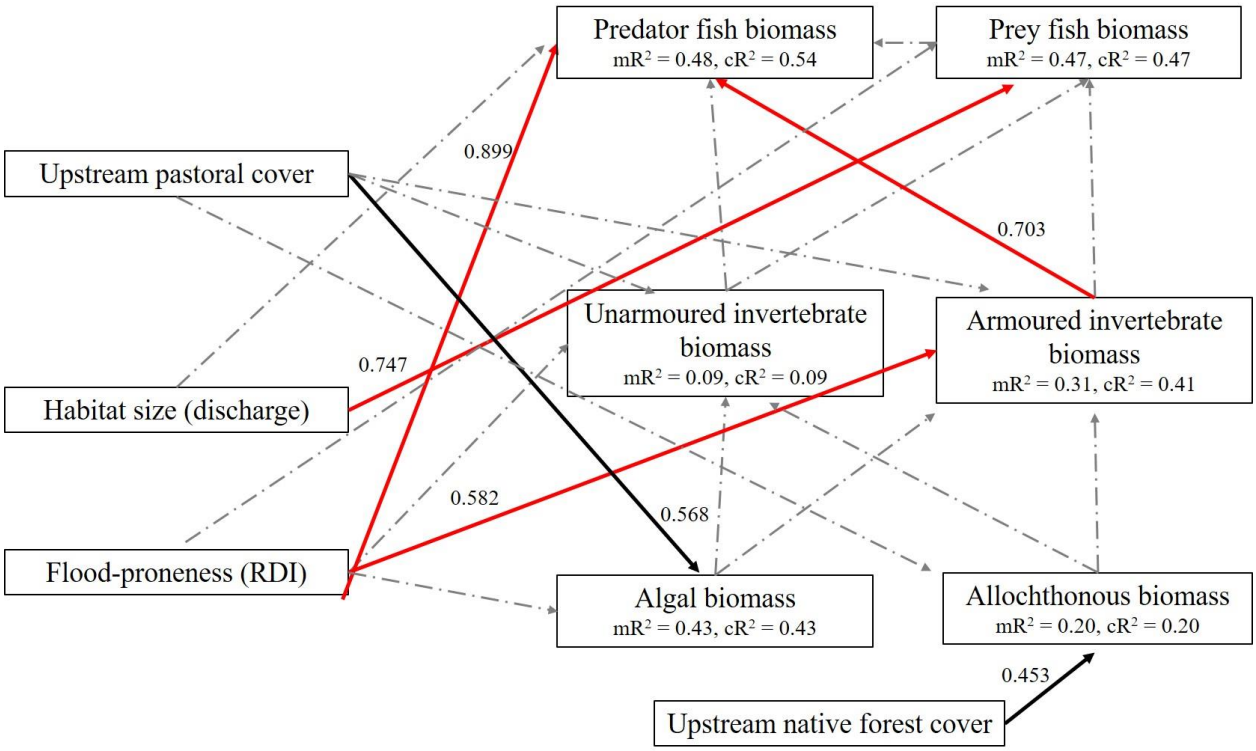

Figure 5.2. Results from piecewise structural equation modelling of invertebrate and fish $\delta^{15}N$ interrelationships. Black arrows denote a significant positive effect, red arrows a significant negative effect, and dashed gray arrows indicate no significant effect. Marginal R^2 (mR^2) and conditional R^2 (cR^2) are reported for endogenous variable component models (within boxes), while parameter estimates are included for significant model paths. See 'Methods' for description of variables, and see Table 5.2 for detailed model results.

Furthermore, increased upstream native forest cover (*H3*) was positively associated with biomass of coarse allochthonous matter (Figure 5.3e). This indicates that heavily forested and unimpacted catchments had increased inputs of leaves, sticks, and other detritus to streams compared to less-vegetated or agriculturalised catchments. Additionally, there was a significant positive effect of upstream pastoral cover on algal biomass (*H3*), but no significant effects of pastoral cover on the biomass of any other ecosystem components (Table 5.1 and Figures 5.6 and 5.7a). This shows that agricultural influences affected primary productivity in my streams, but had variable or apparently weak influences on invertebrates and fishes. Finally, surprisingly, there were no significant pathways between algal, allochthonous, unarmoured invertebrate, or prey and predator fish biomasses as I predicted

with my model structure. For example, I expected there would be a positive pathway between algal biomass, unarmoured invertebrates, and prey fishes, but this was not the case.

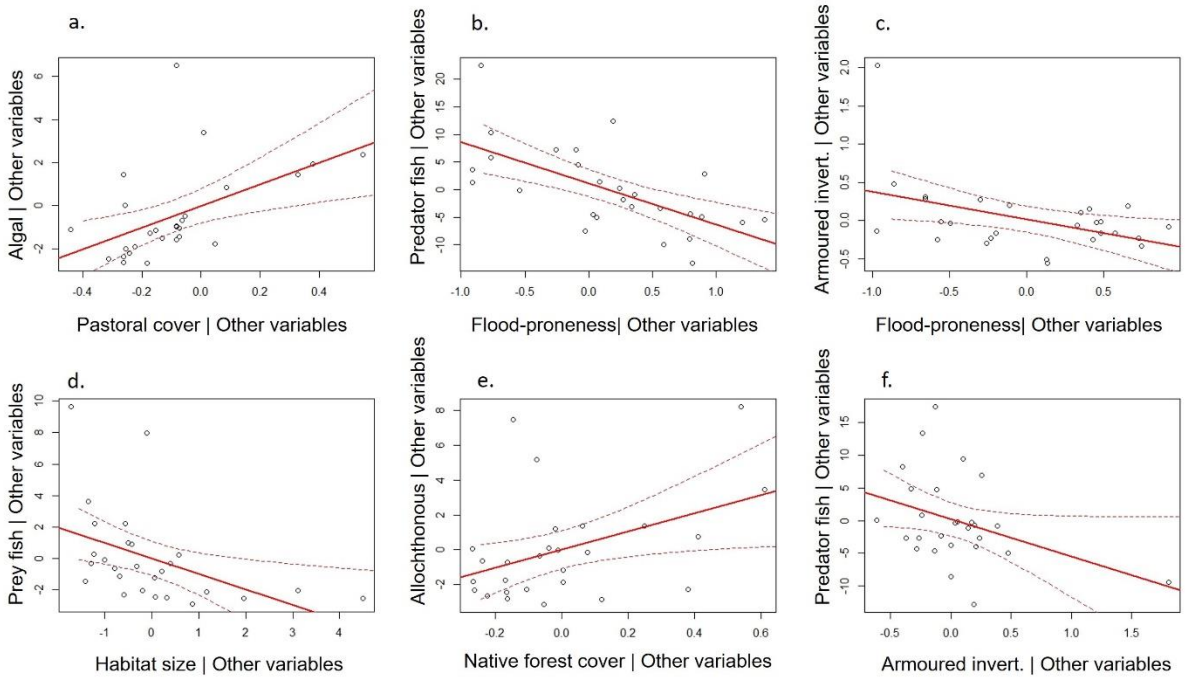

Figure 5.3. Partial residual plots of significant relationships found from structural equation modelling of algal, allochthonous, invertebrate, and fish biomass (all g/m^2), including the effect of percent upstream pastoral cover on algal biomass (a), the effect of flood disturbance (RDI) on predator fish biomass (b), the effect of flood disturbance on armoured invertebrate biomass (c), the effect of habitat size (discharge, m^3/s) on prey fish biomass (d), the effect of percent upstream native forest cover on coarse allochthonous biomass (e), and the effect of armoured invertebrate biomass on predator fish biomass (f). Points are data values corrected for the influence of other predictors as indicated by 'Other variables' in axes labels, red lines are predicted linear regressions, and dashed lines denote 95% confidence intervals for the regression lines. See 'Methods' for description of variables.

Marginal R^2 was good for predator fish, prey fish, and algal biomass component models, fair for armoured invertebrate and allochthonous biomass, and poor for unarmoured invertebrate biomass within the SEM (Figure 5.2). Conditional R^2 was not markedly higher than mR^2 in most cases, indicating that the fixed effects within the model did a good job of

explaining variance in the data, and that spatial factors captured in the random effect did not significantly add to explanatory power.

Nitrogen stable isotope SEM

Similar to the biomass model, a Fisher's C-test confirmed that the piecewise SEM model structure I tested for SI-derived trophic height (Figure 5.4) was appropriate for the data (*p*-value = 0.41, above the 0.05 cutoff value suggested by Lefcheck 2016). In order of hypotheses, model results showed flood disturbance (*H1*) negatively affected predator fish $\delta^{15}N$ (Figure 5.5d), but did not have a significant effect on prey fish $\delta^{15}N$. This suggests that large predator fishes in flood-disturbed streams were forced to feed lower in the food chain compared to their cohorts in stable streams. Other pathways that were tested, but showed no significant effects include a link between habitat size and fish $\delta^{15}N$ (*H2*), and a link between prey fish $\delta^{15}N$ and predator fish $\delta^{15}N$. Thus, it appears that the size of a stream did not influence feeding behaviour and trophic height of fishes, and piscivorous fishes were not clearly linked to the small-bodied fishes within the same reach.

Table 5.2. Standardised component model results from the structural equation model for invertebrate and fish $\delta^{15}N$ from sampling reaches of Canterbury streams. Parameter estimates relate to the magnitude of the predictor on the component model response, and *p*-values denote the significance of the predictor on the component model response (*p*-value cutoff < 0.05). Marginal (mR^2) and conditional (cR^2) R^2 are also reported.

Component	mR^2	cR^2	Predictor	Parameter	Standard	*p*-value
Predator Fish $\delta^{15}N$	0.66	0.69	Flood disturbance (RDI)	-0.69	0.16	<0.01
			Pastoral cover	0.15	0.19	0.43
			Deleatidium $\delta^{15}N$	-0.09	0.16	0.57
			Prey fish $\delta^{15}N$	0.10	0.23	0.66
			Habitat size (discharge)	-0.03	0.13	0.79
Prey Fish $\delta^{15}N$	0.73	0.73	*Deleatidium* $\delta^{15}N$	0.37	0.13	0.01
			Pastoral cover	0.40	0.15	0.02
			Flood disturbance (RDI)	-0.21	0.14	0.15
			Habitat size (discharge)	-0.15	0.11	0.18
Deleatidium $\delta^{15}N$	0.29	0.29	Pastoral cover	0.53	0.22	0.03
			Flood disturbance (RDI)	-0.04	0.22	0.87

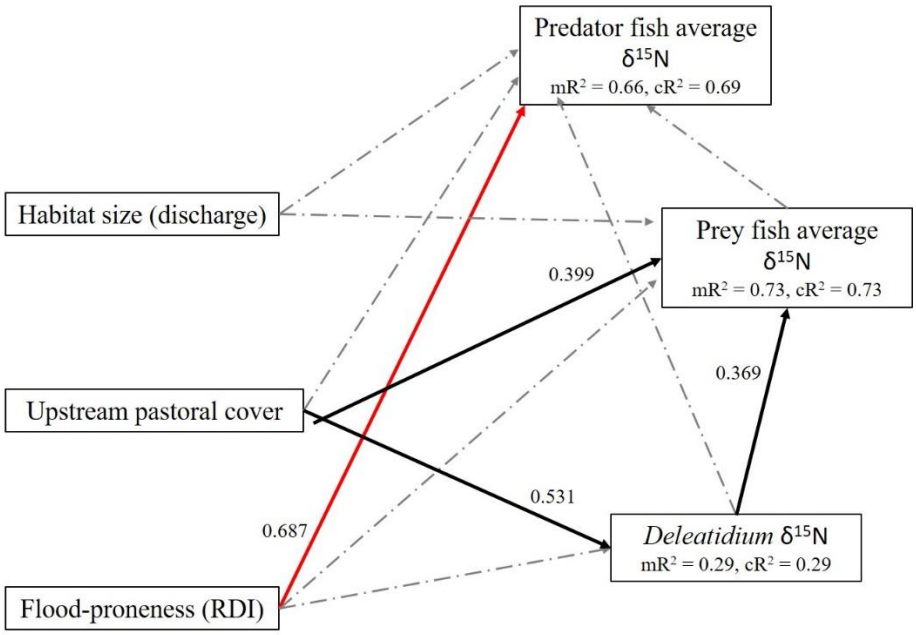

Figure 5.4. Results from piecewise structural equation modelling of invertebrate and fish $\delta^{15}N$ interrelationships. Black arrows denote a significant positive effect, red arrows a significant negative effect, and dashed gray arrows indicate no significant effect. Marginal R^2 (mR^2) and conditional R^2 (cR^2) are reported for endogenous variable component models (within boxes), while parameter estimates are included for significant model paths. See 'Methods' for description of variables, and see Table 5.2 for detailed model results.

Furthermore, there was a significant direct positive effect of upstream pastoral (*H3*) cover on prey fish $\delta^{15}N$ (Table 5.2, Figures 5.4 and 5.5a). Additionally, there was an indirect effect of pastoral cover on prey fish through *Deleatidium* $\delta^{15}N$, whereby pastoral cover boosted *Deleatidium* trophic values (Figure 5.5b), and increased *Deleatidium* $\delta^{15}N$ values were associated with higher prey fish $\delta^{15}N$ (Figure 5.5b). However, there was no significant corresponding effect of pastoral cover or *Deleatidium* $\delta^{15}N$ on predator fish $\delta^{15}N$. Thus, pastoral land cover appeared to influence the trophic values of small-bodied fish through multiple food-web pathways, including indirectly via aquatic invertebrates as I measured, and also through a puzzling direct effect.

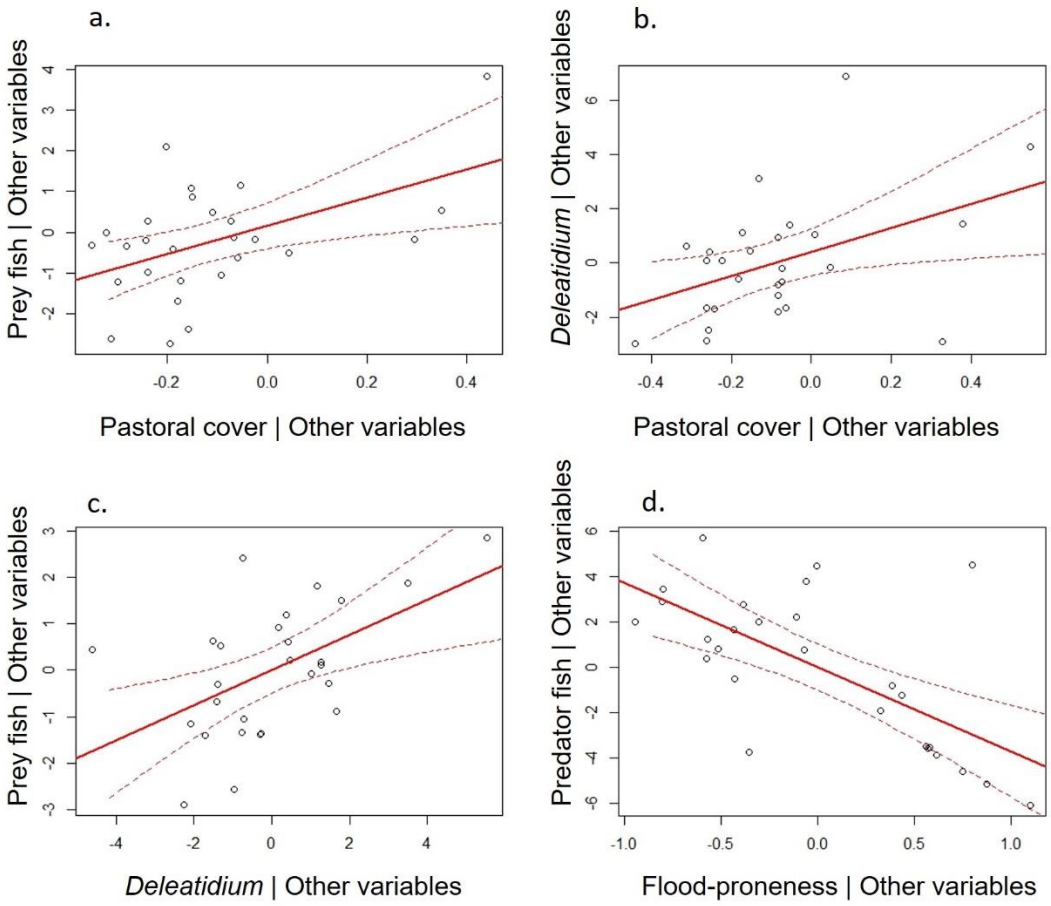

Figure 5.5. Partial residual plots of significant relationships found from structural equation modelling of invertebrate and fish $\delta^{15}N$, including the effect of percent upstream pastoral cover on prey fish $\delta^{15}N$ (a), the effect of pastoral cover on *Deleatidium* spp. $\delta^{15}N$ (b), the effect of *Deleatidium* on prey fish $\delta^{15}N$ (c), and the effect of flood disturbance (RDI) on predator fish $\delta^{15}N$ (d). Points are data values corrected for the influence of other predictors as indicated by 'Other variables' in axes labels, red lines are predicted linear regressions, and dashed lines denote 95% confidence intervals for the regression lines. See 'Methods' for description of variables.

Marginal R^2 was high for both predator and prey fish component models, and fair for *Deleatidium* within the SEM (Figure 5.4). Conditional R^2 was not markedly higher than mR^2, indicating that the fixed effects within the model did a good job of explaining variance in the data, and that spatial factors captured in the random effect did not significantly add to explanatory power.

Discussion

As expected from my findings in the previous chapters, and the findings of others (e.g., Wootton et al. 1996; McHugh et al. 2015), I found that flood disturbance, habitat size, and land cover influenced SI-derived trophic height and biomass of stream communities. However, there were several differences in the manner SI-derived trophic metrics and community biomass were influenced by abiotic and biotic factors, which shows that while one of these metrics (e.g., predator fish trophic height) can be affected by changing conditions in the stream ecosystem, a similar effect may not register in the other (e.g., predator fish biomass). This is useful knowledge for fisheries and stream managers because the manner in which a perturbation to an ecosystem alters SI-derived trophic interactions and community biomass could have implications for monitoring and management of stream communities.

Flood disturbance (H1)

Several of the predicted trophic pathways from Appendices 5A and 5B were supported as expected. In particular, flood disturbance had a strong negative influence on the trophic height and biomass of predator fishes, and the strength of the various pathways associated with this effect gives some information about the main drivers. The negative effect of flood disturbance on predator fish trophic height was likely due to increasing harshness of habitats that are prone to flooding disturbance (Scrimgeour & Winterbourn 1989; McHugh et al. 2010), which could be causing predator fish to engage in less piscivory. This may be due to the difficulty of locating 'prey' fishes in flood-disturbed reaches because of common flood avoidance behaviours by prey fishes (e.g., interstitial burrowing, Davey et al. 2006) resulting in these prey being less-available or harder to locate and capture as compared to prey in stable stream reaches. Alternatively, 'predator' fish may be feeding more on primary consumers relative to intermediate consumers and first-order predators in flood-disturbed

reaches. This could be due to higher availability of primary consumers compared to intermediate predators in flood-prone reaches (McHugh et al. 2010), and because drift of small, low trophic-level invertebrates during flooding disturbance is high (thus they are readily available for drift-feeding predators, Gibbins et al. 2007). These findings suggest that flooding decreases large trout and eel biomass due to harshness (i.e., causes larger fish to vacate flood-prone reaches), and also changes their feeding behaviour, involving different trophic pathways. Based on the strong effect of flooding that translates to both biomass and SI-derived trophic height, I conclude that flood disturbance is one of the most important factors influencing stream communities, particularly large fishes within them.

Interestingly, there was no corresponding effect of flood disturbance on prey fish trophic height or biomass, probably because prey fishes were predominantly native species (77%) that are adapted to flooding disturbance magnitude and frequency in New Zealand (Davey et al. 2006), and thus their feeding behaviour and trophic height were likely less-affected than predator fish, over half of which were non-native trout. However, this is inconsistent with the findings of McHugh et al. (2012), who concluded that an interaction between flooding and trout presence did somewhat negatively affect the trophic status of native fishes. The discrepancy between my findings and those of McHugh et al. (2012) may be due to milder flooding during the year I sampled, thus streams may have been less harsh and there would have been fewer changes in feeding behaviour of prey fish (thus no trophic height or biomass response). Additionally, McHugh et al. (2012) looked only at differences between trout and *Galaxias* sp. rather than between multi-species piscivorous and non-piscivorous groups as I did, which may contribute to the differences between our findings.

Increased flood disturbance also decreased the biomass per m^2 of armoured invertebrate taxa. This was probably due to vulnerability of Gastropods and cased Trichoptera to dislodgement and crushing from high velocity flows and stream bed

movement that is common during floods (Scrimgeour & Winterbourn 1989; Death & Winterbourne 1995; Wootton et al. 1996). In contrast, unarmoured invertebrates were not significantly affected, most likely because these taxa are more mobile, they can drift readily (e.g., *Deleatidium* in Sagar & Glova 1992), can more easily take shelter from flooding effects, and are thus less-likely to be physically damaged by stream bed movement. However, algal biomass was not negatively affected by flood disturbance. This could be attributed to time-since-last-flood effects, because while periphyton is readily scoured from the streambed during floods (Death 2003; Tonkin & Death 2012), it can rapidly regrow and gain a significant standing stock if there is respite from flooding (Biggs & Close 1989). Recolonization of periphyton may be faster post-flood than that seen with invertebrates or fishes, hence the lack of a strong relationship between algal, invertebrate, and fish biomass in the streams I sampled.

Habitat size (H2)

Contrary to my expectations, habitat size had no effect on SI-derived trophic height of prey and predator fish or predator fish biomass per unit area, although it did negatively affect prey fish biomass. The decrease in biomass of prey fish may be a result of a relative decrease in suitable habitat for small-bodied benthic fishes because higher discharge habitats have midstream zones with high water velocity and depth that may be too swift for small fishes to occupy (e.g., upland bully aversion to areas of high water velocity, Jowett & Richardson 1994). Thus, in large streams, prey fishes may only utilize edge habitats with lower velocities, and biomass averaged over the entire area of a stream reach would be lower than in smaller streams with a higher percentage of suitable habitat.

Comparing the lack of effect of habitat size on predator fishes, large-bodied trout often occupy deep habitats and can cope with higher water velocities (Fraley et al. 2018) while large eels are also commonly found in deep pools (Jellyman et al. 2003), so a negative

effect of habitat size as found with prey fish would not be expected. However, I hypothesized that larger habitats would have increased biomass of predator fish per m^2 because overall there would be more productive space and prey options, but this was not the case. A possible explanation for this may be that total predator fish biomass in a larger stream reach was higher, but biomass per unit area was not significantly different from that in smaller reaches because there was a decrease in prey fish biomass that didn't support increased predator density.

Overall, my findings suggest that larger habitats have lower biomass of small-bodied native fish per m^2, but their feeding behaviour, diet, and trophic pathways are unaffected. In addition, in the streams I sampled, larger habitats did not hold more biomass per m^2 of large-bodied predator fish, nor did habitat size appear to affect predator fish feeding habits or trophic status.

*Catchment land cover (*H3*)*

Following my prediction in *H3*, catchment land cover type influenced both SI-derived trophic height and community biomass. Increased upstream native forest cover resulted in higher coarse allochthonous biomass, likely because native New Zealand beech trees create a dense canopy and shed leaves, bark, and sticks in profusion (Winterbourn 1976), which fall into adjacent streams and are transported and accumulate downstream. This finding suggests retaining native forest and preventing alteration of catchment land cover will be important for maintaining natural allochthonous resource levels. Furthermore, increased upstream pastoral cover positively influenced algal biomass and trophic values of prey fish. The increase in algal biomass associated with pastoral cover was likely explained by a boost in primary productivity due to eutrophication caused by nitrate pollution from agricultural runoff (Graham et al. 2015). However, the influence of pastoral cover on trophic values is probably not due to pastoral cover modulating prey fish feeding behaviours or altering trophic

pathways, but rather is an effect due to nitrate pollution from agricultural runoff on invertebrate and fish tissue nitrogen enrichment. This has been suggested previously by Clapcott et al. (2012) for invertebrates, and I have found evidence of this in other investigations (see Appendix 4B).

Nitrate pollution and enriched nitrogen isotopes from livestock faecal matter and fertilizer that enter streams near pastoral lands are likely taken up by primary producers and filter feeders in streams (Clapcott et al. 2012), which are then consumed by primary consumers such as *Deleatidium* mayflies. Thus, *Deleatidium* take up enriched nitrogen, and prey fish likely bioaccumulate enriched nitrogen when they consume *Deleatidium* and other primary consumers. This likely explains the indirect mechanism through *Deleatidium* whereby pastoral cover affects prey fish nitrogen isotope ratios. However, it is unclear how prey fish may be directly affected by nitrate pollution from pastoral cover as I found in my model. Possible explanations are that prey fish are directly ingesting organic matter that contains enriched nitrate from agricultural runoff, or they are utilizing trophic pathways I did not measure (e.g., terrestrial insects). Additionally, it is surprising that predator fish trophic height was not similarly affected by pastoral cover. This may be due to predator fish eating fewer baseline consumers such as *Deleatidium* in these streams, or that large predators can be more mobile so they travel between streams (Jellyman & Sykes 2003; Young et al. 2010) and thus are less-connected to the upstream land cover characteristics of any single area. Finally, pastoral cover also did not affect either armoured or unarmoured invertebrate biomass, despite conditions for armoured invertebrates often being optimized in agricultural streams (i.e., slow water velocity and high sediment cover; Wootton et al. 1996; Graham et al. 2015) while unarmoured taxa usually suffer because they are more sensitive to poor water quality and lack of streambed interstices (Quinn & Hickey 1990).

Considering the connections I found between land cover type and biota, it is clear that land usage in stream catchments is an important influence on stream community trophic structure. However, much remains to be learned about how agricultural development affects stream trophic webs.

Implications/Recommendations

Based on my findings, I conclude that flood disturbance, catchment land cover, and habitat size are important drivers of freshwater stream communities, and the influence of these abiotic factors seems to be less variable than biotic relationships (e.g., non-significant link between prey and predator fishes). The lack of some biotic relationships may be due to the omission of components or trophic links (e.g., predatory invertebrates), but suggests that stream community structure may be more contingent on abiotic habitat factors. Additionally, I have shown that complementary use of SI-derived trophic metrics and community biomass is a useful method for characterisation of freshwater food webs, as well as for understanding the mechanisms and pathways that affect different ecosystem components. In particular, I was able to draw conclusions that wouldn't have been supported if only one of the responses was analyzed. My models gave me more details about the mechanisms behind how flood disturbance and habitat size may affect aquatic communities and fishes, building upon the work of Sabo et al. (2010), Wootton et al. 1996, and McHugh et al. (2014). Furthermore, it is important that researchers utilizing nitrogen stable isotope analysis in streams with variable pastoral land cover influence be aware of the influence on agricultural-source nitrogen enrichment on their results.

Finally, my findings are likely useful to freshwater resource managers because greater understanding of the mechanisms behind lotic invertebrate and fish trophic structure allows for easier identification of perturbations to communities and may offer solutions to return ecosystems to equilibrium if perturbations are human-driven. My comparison between factors

affecting trophic structure and biomass for predator fish may be useful for managers in New Zealand because trout and eels are important recreational, commercial, and cultural assets that are highly-valued by the public (McDowall 2011; Jones & Closs 2018). Eels are an important traditional Māori food source and are considered ‘taonga’, or an important cultural treasure and a gift from the gods (McDowall 2011). While considered deleterious by some, trout are economically important: international trout fishermen contribute 1-2 million NZD to the economy each year in the Southland region alone (Woolf 2016), and angling for salmonids is ingrained in New Zealand culture. With these considerations in mind, my findings that both biomass and trophic height of large trout and eels are negatively affected by flood disturbance would suggest that recreational and commercial fishery managers should set lower harvest limits for these fishes in flood-disturbed rivers or catchments, to optimize biomass and the number of fish of trophy quality. Conversely, if managers are interested in removing large non-native trout to protect small-bodied native taxa in a stream considered to be critical habitat, an emphasis on maintaining natural flood disturbance regimes or designing natural flows that depress trout biomass could be used to relieve native fish from predation (Chen & Olden 2017). These patterns may also be applicable to other systems globally that have similar fish assemblages and management issues. With knowledge of the mechanisms and patterns affecting freshwater communities and fish assemblages, managers can set harvest limits, regulations, and land-use guidelines that will conserve both the population size of economically important fishes for harvest, as well as maintain biodiversity and community trophic structure in freshwater streams.

Appendix 5A. Rationale for fish and invertebrate $\delta^{15}N$ predicted relationships

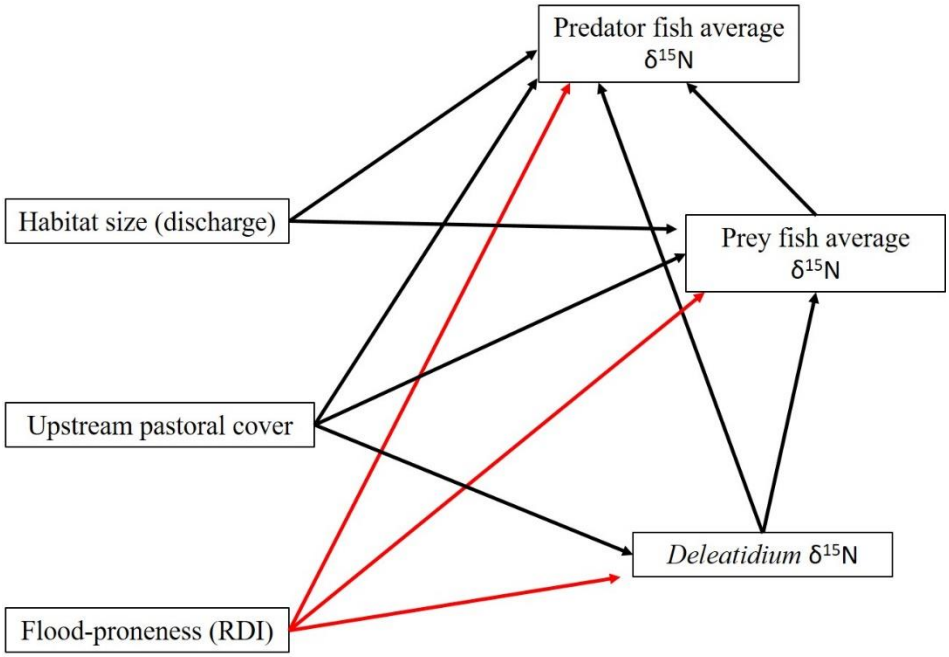

Figure 5A.1 Predicted interrelationships for fish and invertebrate $\delta^{15}N$ tested with a structural equation model. Black arrows denote a positive predicted effect and red arrows a negative effect. See 'Methods' for description of variables, and see 'Box 1' for rationale.

Endogenous response variables (from high to low level) and their effect on other responses

1. Predator fish average $\delta^{15}N$
    a. Top-level response so not predicted to affect other factors in my bottom-up model.
2. Prey fish average $\delta^{15}N$
    a. Affects predator fish ratios positively because predatory fishes are likely consuming prey fishes as part of their diet, which are higher in the food chain than invertebrate prey, contributing to increased nitrogen isotope enrichment.
3. *Deleatidium* $\delta^{15}N$
    a. Affects both prey and predator fishes similarly and positively, because the diet of both fish groups likely contains *Deleatidium* (although different proportions of the diets), and increased nitrogen enrichment in *Deleatidium* prey (due to site-specific variation in primary producer nitrogen isotopes) will translate to increased enrichment for predators (bioaccumulation).

Exogenous (predictor) variables (random order) and how they are predicted to affect endogenous variables

4. Habitat size (discharge)
    a. Affects predator fish positively because there should be more space and more total fish and invertebrate prey biomass available to support larger-bodied fishes, which have increased gape size and are able to consume prey higher on the food chain.
    b. Affects prey fish positively because there should be more area to feed in, which results in increased opportunity to prey upon a higher diversity of items, including invertebrate predators. Prey fish consuming these invertebrate predators that are higher in the food chain than primary consumers should boost fish nitrogen enrichment.
5. Upstream pastoral cover
    a. Following findings by Clapcott et al. (2012) and Chapters 2 and 4 of this thesis), agricultural cover has been shown to artificially increase invertebrate and fish nitrogen enrichment. Therefore, I expect increased upstream agricultural cover will result in overall increased nitrogen enrichment at all levels.
6. Flood disturbance (RDI)
    a. Increased flood disturbance typically translates to a harsher environment, and has been shown to affect primary consumers as well as stable isotope metrics (and thus the diet) of fishes (Chapter Two; McHugh et al. 2014). This is likely due to decreased prey diversity (fewer invertebrate predators at higher trophic positions) and increased energy and time requirements for finding and pursuing prey (of either invertebrate or fish variety), resulting in predators feeding on prey at lower trophic levels and thus exhibiting decreased nitrogen isotope enrichment.

Appendix 5B. Rationale for community biomass predicted relationships

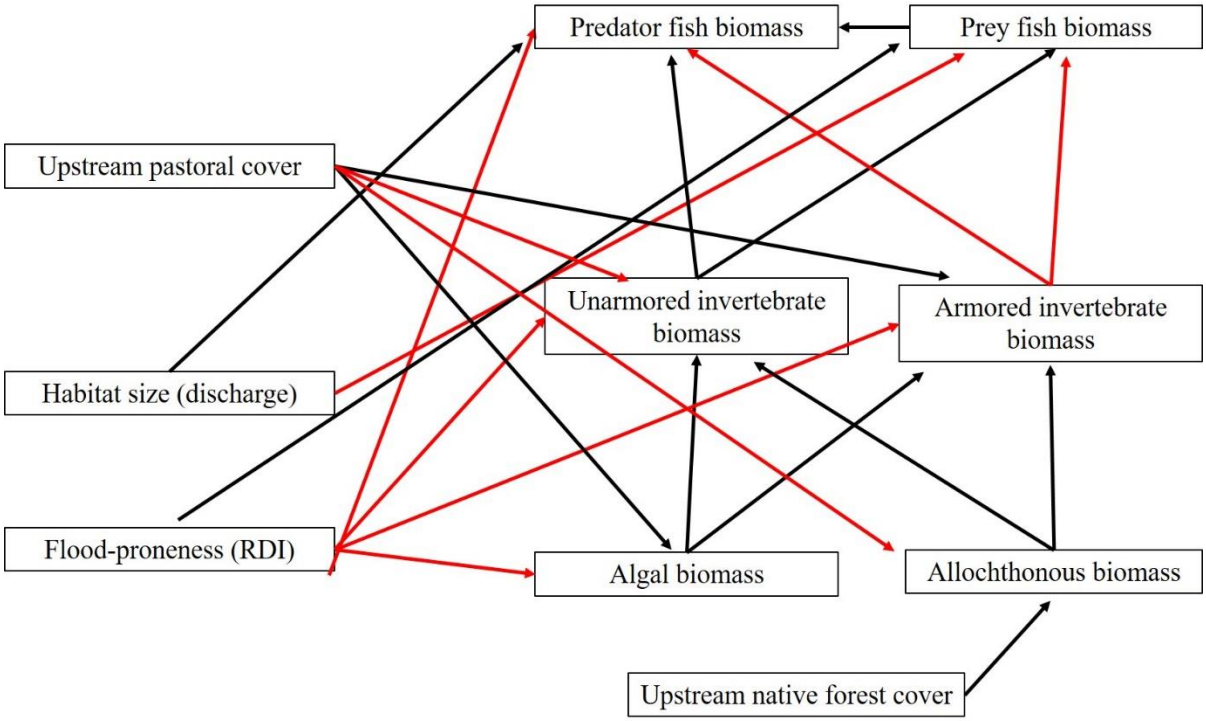

Figure 5B.1. Predicted interrelationships for fish, invertebrate, allochthonous, and algal biomass (g/m^2) tested with a structural equation model. Black arrows denote a positive predicted effect and red arrows a negative effect. See 'Methods' for description of variables, and see 'Box 2' for rationale.

Endogenous response variables (from high to low level) and their effect on other responses

1. Predator fish biomass
    a. Top-level response so not predicted to affect other factors in my bottom-up model.
2. Prey fish biomass
    a. An increase in the amount of prey fishes should support bigger or more numerous piscivorous fishes, increasing predatory fish biomass.
3. Armoured invertebrate biomass
    a. Armoured invertebrates are less-palatable for both prey and predatory fishes, thus an increase in biomass of these taxa would result in longer foraging and processing times for fishes, lowering feeding efficiency and decreasing the carrying capacity for fishes.
4. Unarmoured invertebrate biomass

    a. Unarmoured invertebrates allow for shorter foraging and processing times for fishes consuming them, thus an increase in their biomass should allow for more numerous or larger fishes.

5. Algal biomass
    a. Increased algal biomass should positively affect both armoured and unarmoured invertebrate biomass because both of these groups rely on periphyton for a food source. Thus, more periphyton biomass should result in more numerous or larger invertebrate consumers.
6. Allochthonous biomass
    a. Allochthonous material and associated microfauna should positively affect both armoured and unarmoured invertebrate biomass because both of these groups can utilize allochthonous material as a food source. Thus, more allochthonous biomass should result in more numerous or larger invertebrate consumers.

Exogenous (predictor) variables (random order) and how they are predicted to affect endogenous variables

7. Habitat size (discharge)
    a. Habitat size should increase prey and predator fish biomass because there is more space, more food resources, and more refugia in large habitats to support more numerous and larger fishes.
8. Flood disturbance (RDI)
    a. Increased flood disturbance should negatively affect algal biomass, because of streambed shift and current velocity dislodging and flushing algal mats.
    b. Increased flood disturbance should negatively affect both armoured and unarmoured invertebrates (although at different magnitudes) because strong current and streambed shift during flooding dislodges and flushes invertebrates, or makes it difficult for them to forage.
    c. Increased flood disturbance should negatively affect predator and prey fish biomass because the harsher environment increases the difficulty of foraging for and pursuing invertebrate or fish prey, and increased current velocity increases the energetic demands placed on fish to maintain position.
9. Upstream pastoral cover

a. Increased pastoral cover should increase algal biomass because sediment and nitrate pollution that occur in these areas artificially boost periphyton growth.
b. Increased pastoral cover should negatively correlate with allocthonous biomass because there is typically less riparian vegetation and less terrestrial input in farmed areas.
c. Increased pastoral cover should increase armoured invertebrate biomass, because gastropods and other taxa within this group are tolerant of sediment and other pollutants.
d. Increased pastoral cover should decrease unarmoured invertebrate biomass because increased sediment pollution in these areas fills in interstitial habitats utilized by this group. Additionally, mayflies, stoneflies, and other taxa in this group are intolerant of pollutants.

10. Upstream native forest cover
    a. Increased upstream forest cover should increase the biomass of allochthonous material in a stream because there will be more terrestrial input (i.e., leaves, sticks, and grasses) in streams with more overhanging vegetation.

Chapter Six

General Discussion

A large longfin eel fin clipped and released in the Okana River during fieldwork for Chapter Five.

Within this thesis I have endeavoured to advance the knowledge of how abiotic and biotic habitat factors affect stream fish assemblage composition and trophic structure. In this Discussion chapter, I recount my major findings, and tie data Chapters together to present important conclusions that are useful for freshwater ecologists and stream resource managers. I also give recommendations on use of stable isotope analysis in streams, based on the salient results from this doctoral research. Finally, I provide recommendations for future research that will build upon my findings and investigate aspects that I was unable to address with my work.

Main Findings

In Chapter Two, I verified the suitability of fish mass–abundance relationships and stable isotope-derived trophic metrics as integrative, functional measures of freshwater stream fish assemblages by demonstrating that they responded to both abiotic and biotic habitat factors. This affirms the usefulness of SI-derived trophic metrics and confirms the assertions by Warburton (2015) and Jennings et al. (2002) that mass–abundance relationships could be employed as proxies for food-web description. One of the most interesting findings from this research was that the presence of large-bodied, predatory, longfin eels drove fish assemblage structure in streams, influencing food-chain length, trophic breadth (carbon range), and mass–abundance slope. This highlights the importance of this sensitive, native species, suggesting that it is a keystone predator and integral to food webs in New Zealand streams. In contrast, while associated with increases in maximum body size and size range within assemblages, the presence of large-bodied, predatory, non-native trout did not significantly influence trophic metrics or mass–abundance relationships. Thus, it appears that trout are unable to replace the ecosystem role of native predators, considered to be declining (Allibone et al. 2009; PCE 2013). Therefore, it will be important for New Zealand stream managers to ensure harvests of longfin eels are sustainable and maintain river connectivity to

facilitate eel migration to conserve eel populations and maintain natural stream ecosystem function.

Other findings from Chapter Two showed that increasing flood disturbance led to small decreases in fish mass–abundance slopes, a result of fewer large-bodied individuals and more small-bodied taxa being present in flood-prone streams. This was likely because of the harsh conditions for fishes that are present in streams with frequent flood disturbance, and similar effects were described by Jellyman et al. (2014). In addition to mass–abundance relationships, I concluded that flood disturbance also negatively affected fish assemblage trophic breadth (carbon range), indicating that fishes in flood prone reaches have more limited prey options compared to those that occupy stable, benign streams. This is parallel to the conclusions of McHugh et al. (2012), who found effects of flood disturbance on carbon trophic metrics, but in the context of trout-*Galaxias* competition rather than fish assemblages as a whole. Furthermore, similar to the contentions of Sabo et al. (2010) and McHugh et al. (2015), I found that increased habitat size was associated with longer food chains. This supports the theory that an increase in productive space can result in greater trophic complexity, which has been contested by some studies (Walters & Post 2008; Warfe et al. 2013). Based on these findings, flood disturbance and stream habitat size are clearly important influences on stream fish assemblages and community trophic structure.

Finally, I found in Chapter Two that riparian land cover type had variable influence on the fish assemblage proxies that I measured. Land cover data has been utilized previously in New Zealand to assess effects on abundance, presence, and diversity of fish taxa (Hanchet 1990; Joy & Death 2004), but has not been analyzed in the context of holistic fish assemblages and stream food webs as I have done here. Most notably, I found that native forest and scrub cover boosted food-chain length, indicating the importance of intact riparian vegetation for stream ecosystem health (Richardson et al. 2007). Native tussock cover was

also positively associated with fish assemblages, correlating with increased size range of fishes and greater trophic breadth, perhaps due to the habitat complexity offered by the stems of this vegetation, and the associated input of terrestrial prey that utilize tussock habitat (Edwards & Huryn 1996). Contrastingly, bare ground riparian cover was associated with decreases in maximum size and biomass within fish assemblages (although not SI metrics), likely reflecting the lower productivity of reaches devoid of terrestrial vegetation (Richardson et al. 2007). These findings show that catchment land cover can affect fish assemblages and stream ecosystem processes, and highlights the importance of intact vegetation in maintaining natural fish assemblage characteristics and community trophic structure.

Next, in Chapter Three, I utilized the newly-vetted mass–abundance relationships, along with SI-derived metrics, to quantify the effects of small-scale water abstractions on stream food webs. This was done via a novel sampling scheme that accounted for natural streambed hyporheic exchange and isolated the effects of abstraction. I found that habitat size reduction downstream of abstraction points resulted in decreases in overall fish abundance, abundance of large-bodied fishes, and food-chain length. This was a result of lower abundances of large-bodied trout and eels in dewatered reaches, with the loss of these top predators explaining the shortened food chains. Support for the negative effect of decreased habitat size on large-bodied fishes was provided by my finding that native fishes were more abundant relative to non-native trout in reaches affected by abstraction, and suggests that trout are less-adapted to cope with reduction and variation in habitat size. Thus, while water abstraction negatively affects large, economically important trout (Woolf 2016), the effects are less-obvious on native *Galaxias* and *Gobiomorphus* species that exhibit strategies for coping with low flows (Davey et al. 2006). These conclusions are supported by a similar study (Leprieur et al. 2006), which focused on the effects of abstraction on trout and a single native species rather than examining the effects on entire fish assemblages as I did. Thus,

managers may be able to tailor low flows (Chen & Olden 2017) and utilize movement barriers provided by some abstraction points to benefit native fish populations under threat of extirpation from trout. However, in this scenario there would still be a need to avoid negative effects of excessive abstraction on native fishes. Conversely, managers should limit water abstraction and elevate low flow limits in streams where trophy trout are sought by anglers to increase the abundance of large-bodied individuals to add value to recreational fisheries. It should be noted that these findings relate to single water abstraction points, but in reality there are often multiple points of abstraction along waterways, and I have discussed recommendations for continued research in this context in the subsequent 'Future Research' section.

In Chapter Four I evaluated the relationship between fish body size and SI-derived trophic position, finding that there was no significant link between the two across the species that I sampled, but there were species-specific relationships. While I was the first to investigate this relationship for temperate freshwater fishes, others have found similar patterns in tropical and marine fishes (Jennings et al. 2001; Layman et al. 2005). However, in contrast to my results, Arim et al. (2010) found a significant across-species relationship between body size and trophic position, although the species they were investigating were all closely-related killifishes. In my research, I found that *Galaxias*, eel, bully, and nonanadromous Salmonidae species all exhibited weak positive relationships between increasing body mass and trophic position, as expected by ecological theory relating to animals that exhibit indeterminate growth (Woodward et al. 2005). I also described an inverse relationship between body size and trophic position for juvenile pre-migratory Chinook salmon, capturing the declining influence of maternal marine-derived nitrogen signatures, which has not been quantified previously. These findings show that there is a weak relationship between body size and trophic position for most species, but unquantified

differences in species-specific morphological and metabolic factors obscure any overall relationship across the taxa that I measured.

In addition to effects of body size, I also found that the abiotic habitat factors I identified in Chapter Two significantly influenced the trophic position of certain species (Chapter Four). Thus, I showed that environmental influences, in addition to body and gape size, can affect trophic pathways (and likely the diet) of fishes. Specifically, flood disturbance had a negative effect on small-bodied, benthic bully species, causing them to feed lower in the food chain. Again, this is likely a result of the harshness of flood-prone environments, where prey is typically less abundant, less diverse, and more difficult to capture for some fishes. Interestingly, I found that decreasing habitat size positively affected the average trophic position of nonanadromous Salmonidae species, in contrast to food-chain length (maximum trophic position) findings made by others (McHugh et al. 2015) and in Chapters Two and Three of my thesis. I attribute this result to increased piscivory of trout in small streams, or to the potential isotopic influences of unmeasured terrestrial-source prey that are more likely to be available in narrower streams. While I did identify some factors that influence trophic position of freshwater fishes, the explanatory power of my models was low, suggesting complicated interactions between fish body size, the environmental factors I tested, and other habitat factors yet-unquantified. I have provided recommendations for further investigation of these possible 'other' habitat factors in the subsequent 'Future Research' section.

Finally, in Chapter Five I quantified community biomass and average SI-derived trophic height for fish and aquatic invertebrates, identifying interrelationships between community components, some of which held true for both biomass and SI-derived trophic structure models. An integrative analysis combining both biomass and SI-derived trophic height across multiple components of a food web has not been previously undertaken in

freshwaters, although McHugh et al. 2010 did look at invertebrate biomass and SI metrics in a much more limited manner. Thus my findings are useful for ecologists and stream managers trying to conserve both food-web structure and fish biomass for optimal fishery management. Flood disturbance was clearly an important driver of both fish trophic pathways and biomass, and negatively affected the average trophic height and biomass of large-bodied, piscivorous trout and eels. These mobile predators were forced to feed lower in food chains if they remained in flood-prone reaches, or they may have vacated them and moved to more benign habitats. Thus, to conserve biomass of large-bodied, harvestable fishes, managers should set more conservative harvest limits and regulations for streams or catchments with a high degree of flood disturbance.

Additionally in Chapter Five, my results showed that while changes in habitat size did not affect the trophic height (and thus diet) of fishes, reaches of increased habitat size (measured as discharge) supported lower biomass per unit area of small bodied, non-piscivorous fish. This is likely because larger reaches with increased discharge and current velocity only provide suitable habitat for small-bodied fishes in edge habitats, outside of the main current (supported in the case of bullies by Jowett & Richardson 1994). Interestingly, and in parallel with findings from Chapter Four and Clapcott et al. (2012), I also described how pastoral cover in the upstream catchment boosted the nitrogen enrichment of both invertebrates and fishes, likely due to eutrophication and nitrate pollution, as evidenced by a corresponding positive association with algal biomass. Finally, I confirmed the importance of intact native forest for stream ecosystems, as I suggested in Chapter Two, showing that upstream native forest cover was positively associated with instream coarse allochthonous biomass. Thus, protecting or replanting native vegetation in catchments is critical for maintaining natural stream productivity pathways (Richardson et al. 2007).

Overall, this doctoral research advances previous knowledge of habitat influences on stream fish assemblages and trophic structure, and gives freshwater managers additional tools for informing decision-making.

Considerations for Freshwater Stable Isotope Research

Through this thesis research, I have uncovered several considerations that practitioners of stable isotope analysis should consider when examining stream communities. Firstly, I confirmed the suitability of nonlethal fin clips as substitutes for lethal muscle tissue sampling for two sensitive native eel species. I accomplished this following the methods of Sanderson et al. (2009) and Hanisch et al. (2010), who advocated for nonlethal fin tissue sampling of sensitive or endangered taxa. The equations that I developed for *A. dieffenbachii* (Chapter Two) and *A. australis* (Chapter Four) allow for reliable correction between fin and muscle tissue, proving they can easily be used by other researchers in New Zealand to facilitate nonlethal sampling and protect these charismatic native fishes. The largest *Anguilla* spp. individuals are integral for the breeding success and population preservation of these species (Todd 1981), and extracting a small portion of fin tissue is a much more ecologically sound scientific practice compared to euthanization or sublethal muscle punch methods (Schielke et al. 2010).

Additionally, the choice of SI invertebrate baseline taxa is important to obtain accurate trophic position and food-chain length values that are comparable between streams and catchments (McHugh et al. 2015). Furthermore, I found that it is important to verify that the consumer baseline responds similarly to the other taxa being evaluated across gradients of habitat factors. In the case of the *Deleatidium* spp. used in my research, this genera was best-suited as a baseline because it was ubiquitous across the catchments I sampled, and I confirmed that it correlated well with fish $\delta^{15}N$ values for almost all reaches (see Appendix 4.2). However, for several reaches that had high percentages of upstream catchment pastoral

cover, *Deleatidium* appeared to respond differently than fishes, probably because of nitrogen enrichment of the environment due to nitrate pollution, rendering them less-suitable as a baseline consumer. Although the exact mechanisms of these effects are still unclear, researchers should identify and account for agricultural influences on their study streams when using nitrogen stable isotope analysis (Clapcott et al. 2012).

Interestingly, a single stream reach I sampled that consisted almost entirely of small trout in a catchment comprised solely of native forest also showed a divergence between *Deleatidium* and fish isotope values. I attribute this to isotopic influences of terrestrial invertebrate prey, likely abundant and available for fishes at this reach due to the thickly vegetated riparian area (trout are known to heavily utilize terrestrial prey; Cada et al. 1987; Edwards 1995). Consumption of these terrestrial invertebrates would show a different signature from the aquatic *Deleatidium*, thus the mismatch. Therefore, researchers should also consider the potentially confounding influence of terrestrial prey pathways on fish trophic position and food-chain length values in certain habitats and with surface-feeding fishes such as trout (Baxter et al. 2005).

Future Research

During the course of this research, I identified several promising avenues for future investigation, particularly the incorporation of a temporal aspect. All of the sampling I conducted consisted of single events, with no repeated evaluation across seasons or years. Because fish diet, assemblage trophic structure, and use of energy pathways undoubtedly vary between seasons, the patterns that I described in Chapters Two and Five may change over the course of a year. Fishes are known to have different energy requirements and behaviours between seasons, responding to changes in prey availability, water temperature, and reproductive status (Fausch et al. 2002). Additionally, conditions across years (particularly flood periodicity and mean flow) are likely quite different, and analyses at a

multi-year time scale may lend to enhanced conclusions about what drives stream fish assemblages and community structure, or how abstractions affect fishes under different conditions. In the case of stable isotope samples, these offer a snapshot of fish diet or trophic height over a span of several weeks (Sakano et al. 2005), thus there would likely be fluctuations across seasons in isotopic values.

In terms of small-scale water abstractions, I believe that a useful next step in realistically quantifying the effects of these on fish assemblages would be to evaluate multiple, compounding abstractions. While I have identified the impact of single-point surface water takes, in contemporary riverscapes there are commonly multiple abstraction points along each stream (Booker et al. 2016). Thus, it would be useful to expand my sampling design from Chapter Three to include two or more abstraction points in close longitudinal proximity. It would also be beneficial to develop a GIS-linked database of all known water abstractions on New Zealand streams, which could be integrated with the River Environments Classification database (Snelder et al. 2004) for ease of access for researchers and managers, because current abstraction records were difficult to evaluate without resorting to a field visit. In addition, it would be highly useful for stream managers if future research could identify flow percentage thresholds where stream food web or fish assemblage structure is degraded, so that scientifically-backed low flow and abstraction limits could be set for all streams (Booker et al. 2016). It would also be very useful to experimentally test designer flows, via abstraction points, to achieve ecological outcomes (as suggested by Chen & Olden 2017). For example, the relative impacts of abstractions on non-native and native taxa I discussed in Chapter Three could be a basis to test exclusion of non-native trout and protection of small-bodied native fishes. Development of strategies to successfully accomplish this could by employed by managers attempting to protect critical populations of native fishes under threat of extirpation from trout. Alternatively, flows could be

experimentally altered with the objective of maximizing conditions for occupancy of large-bodied trout in order to foster trophy fisheries.

Finally, I would recommend further investigation into the determining factors of fish trophic position. While I found that fish body mass, habitat size, and flood disturbance variably affected the trophic position of fishes, much of the variation in trophic position was left unexplained. While some of this unexplained variation was encompassed in the Stream and Catchment ID random effects within my models, I did not identify the factors that differed between these streams and catchments which drove variation in trophic position. Possible additional factors to explore might include water chemistry, water temperature, turbidity, underlying geology, terrestrial food sources, primary productivity, and prey diversity (Matthews 2012), all of which are known to influence fish diet, behaviour, or isotopic enrichment, and thus trophic position.

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Appendix A: Ngāi Tahu Consultation and Engagement Group Letter of Support

Ngāi Tahu Consultation and Engagement Group

UNIVERSITY OF CANTERBURY
Te Whare Wānanga o Waitaha
CHRISTCHURCH NEW ZEALAND

15/12/2016

Tēnā koe, Kevin

Re: Influence of land cover, flow, and species composition on trophic position and body size of fishes

This letter is written on behalf of the Ngāi Tahu Consultation and Engagement Group. We have read and considered your proposal and acknowledge that this is a worthwhile and interesting project.

It is well considered and the researcher is clear about how they ought to take participants' (cultural) needs into account where applicable.

Thank you for engaging with the Māori consultation process. This will strengthen your research proposal, support the University's Strategy for Māori Development, and increase the likelihood of success with external engagement. It will also increase the likelihood that the outcomes of your research will be of benefit to Māori communities. We wish you all the best with your current project and look forward to hearing about future research plans.

The Ngāi Tahu Consultation and Engagement Group would appreciate a summary of your findings on completion of the current project. Please feel free to contact me if you have any questions.

Ngā mihi
Nigel Harris

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